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ACCELERATION AND VESTIBULAR MECHANISMS

A study of the interaction of angular and linear accelerations on human vestibular mechanisms

by

Michael A. Bodin

SUMMARY

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SUMMARY

Recent developments in high performance aviation and manned space flight have added a considerable impetus to the need for a better understanding of the behaviour of the Vestibular System. The stresses imposed by these environments may affect the balance mechanisms with important implications for the human traveller.

This is the practical background against which the present study is set, but the work itself is essentially of an academic and theoretical nature.

The primary topic of this thesis is the interaction of linear and angular accelerations, studied under laboratory (simulated) circumstances, on human vestibular mechanisms. Theoretical and practical background studies of other experimenters, relevant to this topic, are reviewed.

A series of differing experiments are described which examine the responses to interacting angular and linear accelerations, on human subjects, first during and then after rotation about each of the three orthogonal body axes: yaw, pitch and roll. Responses were compared both when the rotation axis was horizontal and when it was vertical; also, following rotation, when subjects were tilted to various different positions immediately after stopping.

Two main findings emerged:

(i) During rotation a sustained unidirectional compensatory nystagmic response was present when the rotation axis was horizontal but not when it was vertical.

(ii) Following turning both the rate of decay of after-sensations and nystagmus were increased, either when the axis of rotation was horizontal (compared with when it was vertical), or when the subjects were moved from the plane of rotation after stopping.

These observations are discussed with particular emphasis on possible underlying mechanisms which might have brought them about. It is concluded that a direct action of linear acceleration on the dynamic behaviour of the peripheral end-organ is unlikely, and a central interaction mechanism more probable. The nature of such a mechanism is considered. Simple addition/subtraction, proportional change, or alteration in 'gain' theories are rejected, and a theoretical equation which is a

complex variable, exponential in general form, proposed instead. Reasons for this are given, and a simple mathematical model postulated.

Some practical implications of the experimental observations, irrespective of the underlying mechanism, are briefly mentioned.

ACCELERATION AND VESTIBULAR MECHANISMS

A Study of the Interaction of Angular and Linear Accelerations on Human Vestibular Mechanisms

by

Michael A. Bodin

R.A.F. Institute of Aviation Medicine,
Farnborough, Hants.

April 1970

Addendum

It is regretted that owing to a technical fault in the Xerox copying machine the quality of reproduction varies considerably throughout the text. This is unfortunate, but for the number of pages involved it was not possible to gain access to other suitable Xerox facilities in the time available.

Thesis

presented for the degree

of

Doctor of Philosophy

in the Faculty of Medicine,
University of Glasgow.

The work presented in this thesis is original. The author carried out each of the experiments himself, and also wrote many of them up for reports or Journal publication. Normal scientific assistance was received with the conduct of experiments and analysis of data. Written opinions represent the author's own views on the work presented, but have been influenced by discussion of his findings with friends and colleagues.

To

Ellen

CONTENTS

ACKNOWLEDGEMENTS

I wish to express my gratitude to the late Air Vice Marshal W.K. Stewart for originally encouraging this research, and allowing me the facilities of the laboratories at the R.A.F. Institute of Aviation Medicine, Farnborough, Hants, in which to carry it out. Also to Sir Bryan Matthews and his colleagues on the Flying Personnel Research Committee for valuable comments and advice as each stage of the work was completed.

Dr. Alan J. Benson was in charge of the Vestibular Physiology section while this study was undertaken. For practical assistance as a colleague, and continuous invaluable criticism and discussion I am deeply grateful.†

I owe a special debt of gratitude to Group Captain Tom Whiteside, my thesis supervisor, without whose understanding and constant encouragement this work would not have been completed. Similarly Air Commodore P.J. O'Connor gave me advice and encouragement for which I am extremely grateful.

Many people in the Institute of Aviation Medicine assisted with data processing, analysis and preparation of illustrations. In particular it is a pleasure to thank Miss Joan Stuart, Mrs. Margaret Perry, Miss Helen Ferris and her staff (Statistics), the drawing office and photographic section, and Mr. Johnston of the printing department, Royal Aircraft Establishment, for their willing co-operation.

During the completion of this work my wife lived with a recluse and readily sacrificed a very great deal of her leisure time; I can only express my gratitude by dedicating this thesis to her.

---

†Dr. A.J. Benson participated as an assistant in some of the early experiments in this Project. The studies presented are original, however, and were carried out entirely by the writer. Many of them have been published in reports and/or Journals under the authorship of Benson and Bodin, but the order of names has no special significance and was determined solely by alphabetical convention.

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PART 1

INTRODUCTION

PART 1

INTRODUCTION

1. General Background

The study of vestibular behaviour is far from being the 'backwater' sometimes supposed in comparison with other branches of sensory and general physiology. In fact a great deal of work has been carried out in this field, though until comparatively recently much of it was undertaken by a relatively small number of biologists. Apart from the development of clinical test procedures, however, many of these investigators concerned themselves with the properties of animal preparations, rather than the behaviour of the intact human vestibular system. Previous work which is relevant to the present study is summarised in the second part of this section.

With the advent of manned space flight, however, and concomitant rapid developments in high performance aviation, considerable impetus was added to the need for further investigation of vestibular behaviour.

In both of these environments, increasingly "severe" or "unusual" patterns of motion are being encountered, and these

in turn can be associated with undesirable, incompletely understood or potentially dangerous consequences for the human traveller.

Combinations of angular and linear accelerations may develop, for example, which differ substantially both in time course and magnitude from those to which man is usually exposed on the ground, and therefore lie outside the normal functional range of his receptor and perceptual mechanisms. Responses engendered in such circumstances, by stimulation of the vestibular and other sensory receptor organs, are frequently erroneous, conflicting with other veridical information (e.g. vision), and unless disregarded can lead to uncertainty about position, motion or attitude (spatial disorientation), with potentially grave consequences if the pilot allows these illusory perceptions to dictate his control of the vehicle. Something like 25% of fatal aircraft accidents in the 'human error' category have been attributed to pilot disorientation arising in this way (Nuttall and Sandford, 1959). In the space environment, there was much early speculation about possible adverse effects of weightlessness ('zero gravity') and some evidence to justify these fears with early unstabilized rotating vehicles (Bodin, 1966), where complex force/acceleration fields were present. Subsequent American lunar flights have not substantiated these speculations, but the subject is still one

of current interest in bioastronautics, because of the imminent development of manned orbital laboratories which, by rotation to provide artificial 'gravity', will produce highly noxious vestibular environments.

In these circumstances, the vestibular organs will have a prominent role in the aetiology of possible disorientation. Planned aerospace developments, therefore, with their potentialities for very high speed flight and extended manned space flights, have enhanced the need for a fuller understanding of the basic physiological behaviour of this sensory system.

As a consequence of these developments a considerable increase in research, dealing both with pure and applied aspects of vestibular psychophysiology, has occurred in the past few years, particularly in the United States under the auspices of the National Aeronautics & Space Administration. The R.A.F. Institute of Aviation Medicine at Farnborough, however, has been concerned with research and clinical evaluation of vestibular function for a good many years, and the work which constitutes the present study was undertaken as part of this continuing programme. The specific purpose of the study was to examine human vestibular responses to angular motion stimuli in relation to changes in the concomitant linear acceleration vector.

Earlier experimental work, and theoretical considerations which in part influenced the choice of procedures in this study,

will now be reviewed.

2. Experimental Background and Literature Review

The basis of our present understanding of vestibular anatomy and physiology was firmly established over 40 years ago. This early work is well reviewed by Camis (1930) and Howard and Templeton (1966). Studies of particular relevance to this thesis have recently been thoroughly reviewed by Janeke (1968).

Veits (1932) postulated that it was only possible to study vestibular behaviour under unphysiological conditions, while Jongkees (1944) remarked that any stimulus sufficient to produce nystagmus was already unphysiological. There is a good deal of truth in the former statement, but few would agree with the latter, as stabilisation of the retinal image by means of evoked nystagmus must be regarded as a normal function of the oculo-vestibular reflex arc.

Most stimuli used in vestibular studies are directed so far as possible either to stimulate the canals or the otoliths - i.e. each of the sub end-organs (see Part 2) of the vestibular apparatus separately. The extent to which this in fact is possible is a relevant issue in the present study, and many experiments will be described in which both suborgans are intentionally stimulated together - as will be seen, this is not difficult to do (Benson & Bodin, 1965, 1966).

The classical modes of vestibular stimulation are certain post-rotational responses for the canals, and parallel-swing responses for the otolith organs. The former were introduced in principle as they are used today by Barany in 1907, and subsequently modified by Veits (1931). Later Van Egmond, Groen and Jongkees (1948) refined these principles with the introduction of cupulometry. In these methods the rotation stimuli is applied about a vertical axis and responses from the cupulae of a pair of canals in a plane perpendicular to the rotation axis are studied.

It is maintained on the other hand that pure otolith responses can be examined by means of a parallel swing, which supplies an oscillating linear acceleration/deceleration pattern of stimuli (Groen & Jonkees 1947; Philipszoon 1959; Guedry 1965).

These two techniques presuppose, firstly that a pure rotational or pure linear acceleration stimulus only is supplied; or that neither sub-organ responds to the particular type of acceleration which stimulates the other. This point will be returned to in a moment and again in the terminal discussion (Part 6). Assuming for the present the validity of these postulates the above methods have now been used to the point of saturation, where little more information about the stimulus - response behaviour of vestibular end-organs would seem to be obtainable by these means alone. For further studies, therefore, it is necessary

to invoke different theoretical and practical principals, though these do not by any means invalidate the earlier techniques, many of which are still used with great success as the basis of present day clinical evaluation of vestibular function.

The classical concept of vestibular behaviour - that canals and otoliths are separately stimulated by angular and linear accelerations respectively - was propounded almost a century ago by Mach & Breuer (1875). Later, Ewald (1892) proposed that the canals were responsible for nystagmus, which occurred in a plane corresponding to that of the stimulated canals. This theory 'held the field' for half a century, and still provides the working basis for practical clinical procedures today. Convincing work in this field was carried out by Jongkees (1944, 1964, 1966, 1967), Groen & Jongkees (1946), and Philipszoon (1959, 1962). They described the physiological stimulus-response relationship for each sub-organ separately, concluding that otoliths respond to linear accelerations and gravity, not to angular accelerations, and that semicircular canals are stimulated only by angular accelerations.

The alternative view, that this dichotomy of function was not necessarily absolute, marked an important change of emphasis in basic thought, bearing on the fundamental principles of vestibular physiology.

Magnus & De Kleign (1921) were among the first to hold the view that canals could respond to linear as well as angular acceleration, while Bárány (1921) stated that positional nystagmus probably originated in the otolith organs. Maxwell (1923) showed that direct pressure on an otolith produced eye deviation but no true nystagmus - perhaps because the stimulus was a constant rather than a changing one. By contrast, Versteegh (1927) failed to observe nystagmus after destruction of the socculus and utrical nerves. Borries (1925) was the first to use the term otolithic-ocular reflex.

Lorente de Nó (1931) held the view that the physical properties of the membranous canals where such that they could be displaced by linear accelerations, with possible cupular stimulation and generation of nystagmus; while Ter Braak (1936), Grnandt (1950) and Timm (1953) all postulated that the cupula was of greater density than the surrounding endolymph, which would theoretically render it linear acceleration (gravity) sensitive. Likewise Vogel (1951) considered the canals gravity sensitive; Sjöberg (1931) studied the effects of linear accelerations in lifts, and noted suggestions of nystagmus in several of his subjects. Ulrich (1934), however, produced only eye deviations but no true nystagmus, by direct stimulation (proding) of otoliths in unanaesthetised pike; Szentagothai (1952) made similar observations in cats and dogs. Removal of the pike otoliths, however,

produced neither eye deviations nor nystagmus.

Grabiel et all (1952) were unable to produce nystagmus by exposing subjects to an increased resultant linear acceleration in a centrifuge. Benson & Whiteside (1961), however, showed a significant suppression of nystagmus engendered by the angular acceleration of a centrifuge at high linear (centrepetal) accelerations (3.1g); a result attributed either to a direct influence of the acceleration on cupular deviation, or to a central modification of ampullary input mediated through the otoliths. Whatever the reason, the stimulus was highly unphysiological, and interpretation of the findings correspondingly open to question.

A number of surgical studies, involving sectioning the utricular nerve in cats, have been carried out, but the results have proved equivocal. Versteegh (1927), Jongkees (1950), Fernandez et al (1959) were able to produce spontaneous ~~(though not to elicit)~~ nystagmus; in contrast, Sullivan et all (1957) did not find post-operative spontaneous nystagmus.

Benson & Whiteside (1961), Benson (1962), Benson & Bodin (1965,1966a & b) and Bodin 1967 & 1968 (unpublished) postulated that differences in specific gravity between endolymph and perilymph could render the canals gravity sensitive.

This concept was based initially on the observation that human subjects rotated at constant velocity about a horizontal

cephalo-caudal body axis exhibited sustained lateral nystagmus (Benson & Bodin, 1966). Subsequently these workers abandoned the hypothesis in favour of a central interaction effect between signals from otolith and ampullary receptors. Experiments in which electrodes were implanted in the brain stem nuclei of cats moved in a circle on a counter-rotating platform played an import role in this change of view (Benson, Guedry & Melville Jones, 1967). Two other major studies were also incompatible with Bodin & Benson's hypothesis. Money (1968) rotated cats about a cephalo-caudal earth vertical and earth horizontal axis, following surgical blocking of all six semicircular canals, and showed that in the latter situation nystagmus during constant velocity rotation was modified but not abolished. He concluded that the otoliths played a dominant role in production of the effect. Janeke (1968) produced further strong evidence, supporting Money, when he showed that destruction of the saccules and utricular nerves in rabbits, but leaving the canals intact, abolished the response entirely. He regarded this as proof that the canals are not gravity sensitive or act as linear accelerometers in any way.

If this view is correct, there is no difficulty in explaining earlier observations in which nystagmus was apparently evoked by pure linear acceleration stimuli. Jonkees & Philipszoon (1961, 1962), Bos et al (1962) and Jonkees (1964), for example

produced nystagmus both in rabbits and humans on a parallel swing. These workers, and others, noted that a parallel swing provides an otolith stimulation (Jongkees 1944, 1964, 1966; Groen and Jongkees 1946; Niven et all 1966), though they did not always attempt to draw the conclusion that it was this which produced the nystagmus.

The findings of Money (1968) and Janeke (1968) seem conclusive enough, but there is still some room for argument. For example, the canals and otolith anatomically (see Part 2) form a closed water tight system, and it cannot be said unequivocally that surgical interference with one, however carefully carried out, cannot modify indirectly the function of the other. Nor can conflicting experimental findings, unless techniques are faulty, simply be ignored, even though later work fails to confirm them. Money (1965, personal communication) performed a similar experiment to above, though on a much smaller scale, and found that nystagmus was abolished by surgical blocking of the semicircular canals; Yokoyama (1965) subjected rabbits and humans to changing linear accelerations, and obtained only counter-rolling and eye deviations but no true nystagmus, thus substantiating the classical hypothesis connecting eye-movements with the otolith (Nagel, 1896). Benson 1965, Howard and Templeton 1966, and Yaneke 1968, among others, have reviewed past and present views on physiology of canals and

otoliths. The present brief review is intended only to show that while modern evidence is tending towards the belief that canals do not respond to linear accelerations, and otoliths may produce nystagmus, there are still a number of open questions and conflicting views which require to be reconciled.

It is generally accepted, however, if we disregard for the moment the full consequences of vestibular stimulation, that the canals are dynamic receptors, responding to angular accelerations, while the otolith organs subserve both dynamic and static functions depending on position and rate of change of position (Part 2) (Ross, 1939; Adrian, 1943; Lowenstein and Roberts, 1949).

The vexed question of nystagmus is perhaps best regarded as well, but not fully, understood, and will be returned to in the final discussion (Part 6). Meantime, the views of Jongkees & Philipszoon (1962) who combined 'the best of both worlds', are worth noting. Nystagmus has two components, a slow and a fast phase. Each of these has its own threshold. When the eye is deviated, either by a cupular or an otolith stimulation, the threshold for a quick repositioning ("saccadic" - Guedry, 1964) movement is reached and so a nystagmus beat is formed. There is probably much truth in this simple exposition. What still requires to be clarified is the role of otoliths in modifying

or initiating regular repetitive nystagmic eye-movements.

The present study describes a series of related experiments undertaken by the author, using 'physiological' stimuli (contrast some earlier work and animal investigations), designed to examine the influence of a 'lg' linear acceleration on vestibular responses to angular motion. It stems directly from the earlier work at Farnborough of Benson & Whiteside (1961), and aims to evaluate the contribution of canals, otoliths and central interaction effects in the genesis and modification of evoked nystagmus.

The experiments are first discussed in relation to one another and then in the wider context of their relation to other concurrent laboratory studies reviewed above. This work was carried out during the period 1964 to 1968.

PART 2

ANATOMY AND PHYSIOLOGY OF THE VESTIBULAR APPARATUS

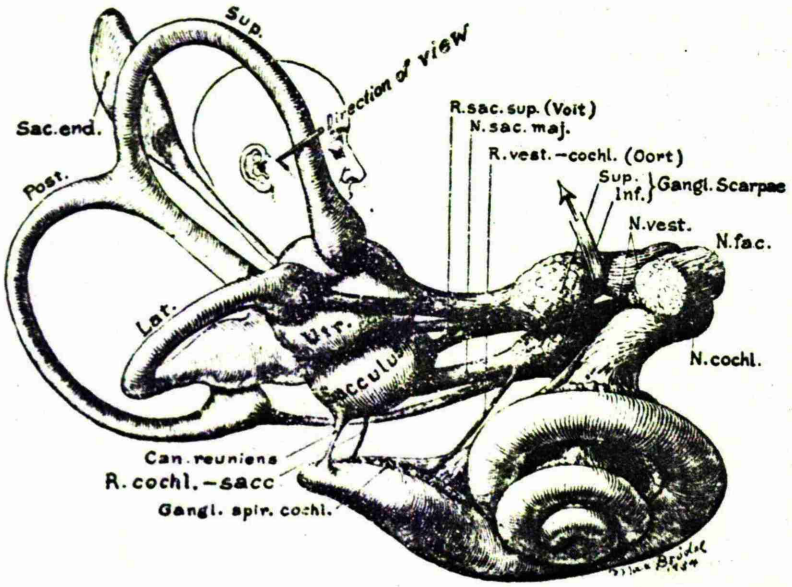


Figure 2.1

Diagram of the right vestibule. The vestibular nerve, ganglion and cochlea are also shown. Note orientation of the canals, with the lateral canal inclined 30^{o} upwards anteriorly when the head is in the normal upright position.

PART 2

ANATOMY AND PHYSIOLOGY OF THE VESTIBULAR APPARATUS

There are numerous books which describe the structure and function of the vestibular organs. Howard and Templeton (1966) and Benson (1965) give particularly clear accounts. The following brief review of salient factors is taken mainly from these sources.

The Vestibular apparatus, together with the cochlea form the membranous labyrinth (Fig 2.1). This is situated in a 'form fitting' cavity in the petrous part of the temporal bone - the so called bony labyrinth. The vestibular part is made up of the three semicircular canals, which lie superior to and communicate with the utricle, below which is the saccule. The whole system is filled with fluid (endolymph), and also surrounded by fluid (perilymph) which occupies the space between the membranous and bony labyrinth. The membranous canals occupy not more than about one third of the available space within the bony canal, and appear to be tethered to it at only one point around their circumference; the remaining space contains flimsy strands of connective tissue, extending between the walls

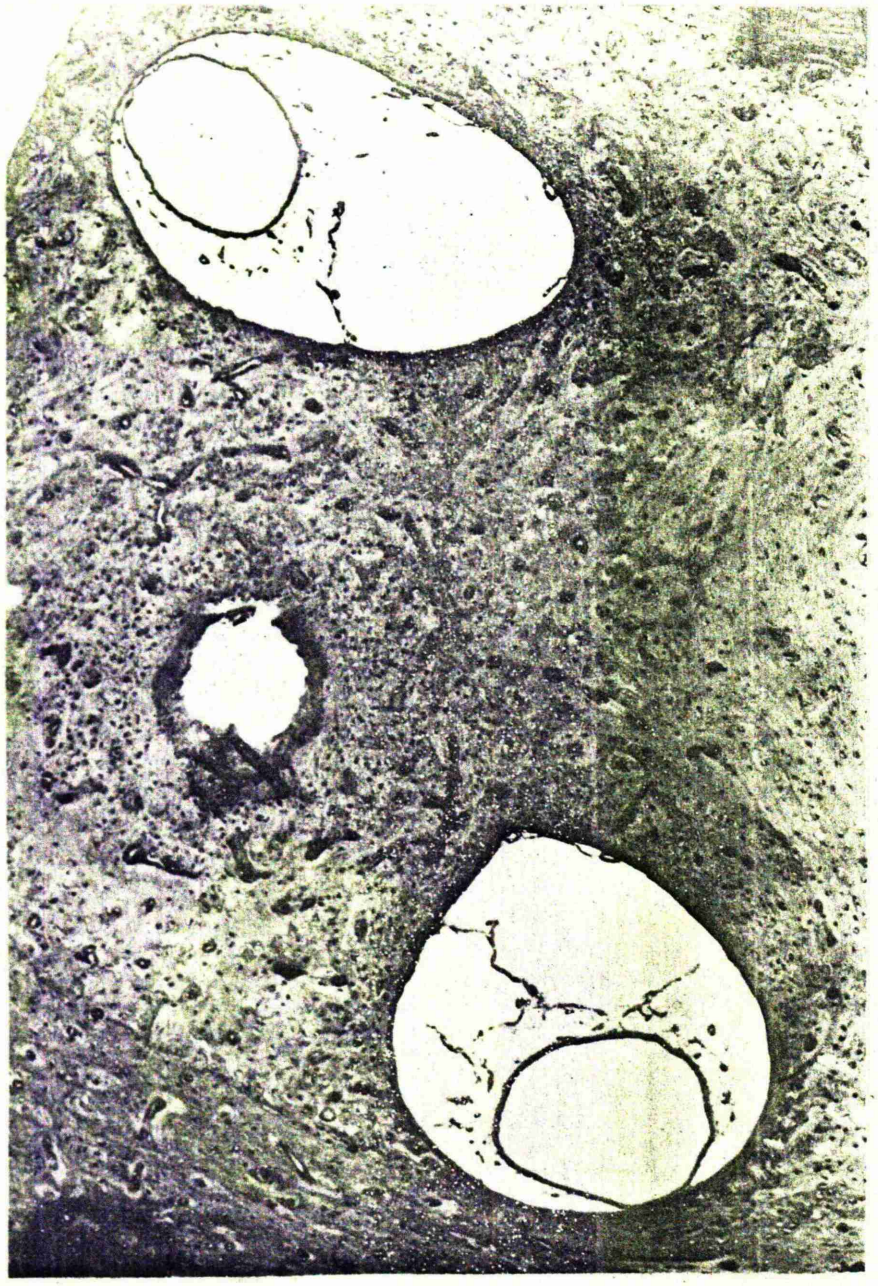


Figure 2.2

48x enlarement of a Haematoxylin-phloxin stained oblique frontal section through the superior and lateral canals of a rabbit vestibule, fixed by intra-arterial perfusion. Note that the membranous canal, about 0·5 mm. (actual) diameter, occupies a small part of the available space within the bony canal, and is attached to it only at one point on its circumference. The remaining space appears filled with loose connective tissue strands, distorted on sectioning.

(Courtesy of Dr. J. James, University of Amsterdam.)

of the membranous and bony canal (Fig 2.2). The arrangement is such as to suggest that there is considerable scope for movement or deformity of the smaller membranous canal within the bony canal.

The sensory epithelium of the semicircular canals lies in a dilatation or ampulla, heaped up to form a ridge known as the crista (Fig 2.3). Each sensory cell has several hair-like projections arising from it (Fig 2.4) and these pass into the substance of the cupula, which surmounts the crista as a flap like structure occluding the ampulla, yet free to swing to and fro in the manner of a watertight partition hinged at its base (Steinhausen, 1931). As the canals move in space the inertia of the endolymph generates asymmetric forces which deviate the cupula and so alter the rate OF FIRING of the sensory cells. These forces are associated with angular accelerations in the plane of the canal, the three pairs of canals being so positioned that the ampullary receptors of at least one pair are stimulated whatever the plane of the imposed motion. The rate of firing of the sensory cells is thought to be governed by the mechanical deformation of the kinocilia, though the method of electro-mechanical transduction is not understood. The stereocilia on the other hand play no direct part in this process, but serve to support the cupula and supply the elasticity which provides a

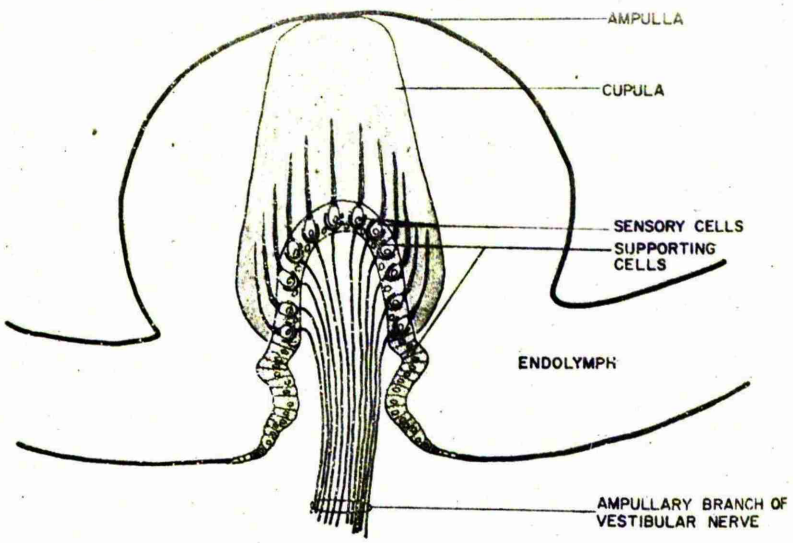
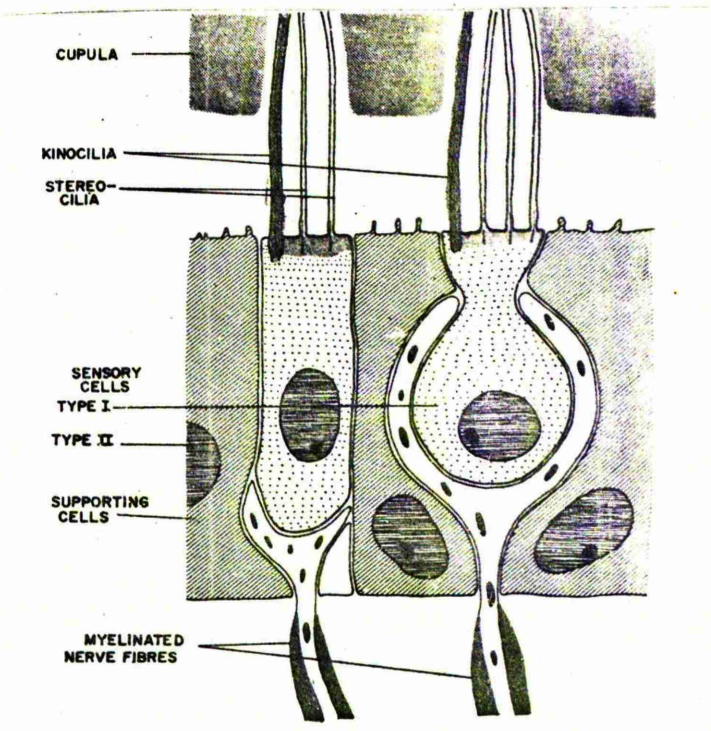


Figure 2.3

Diagram of the ampulla of a semicircular canal sectioned in the plane of the canal. The hairs of the sensory cells in the crista pass into the substance of the cupula, which surmounts it as a water tight flap extending across the ampulla.

Figure 2.4

Simplified diagram of the cells found in the crista ampullaris. The rate of firing of the sensory cells is thought to be governed by the mechanical deformation of the kinocilia. The stereocilia support the cupula and provide the restoring couple when it is deflected.



restoring couple when it is deflected. If all the forces acting on the cupula are considered, its subsequent behaviour following an angular acceleration stimuli may be described by a second order differential equation, similar to that of an overdamped torsion pendulum (Steinhausen, 1931):

$$H\ddot{x} + \pi\dot{x} + \Delta x = 0$$

where H = moment of inertia of the cupula.

π = moment of friction per unit angular velocity.

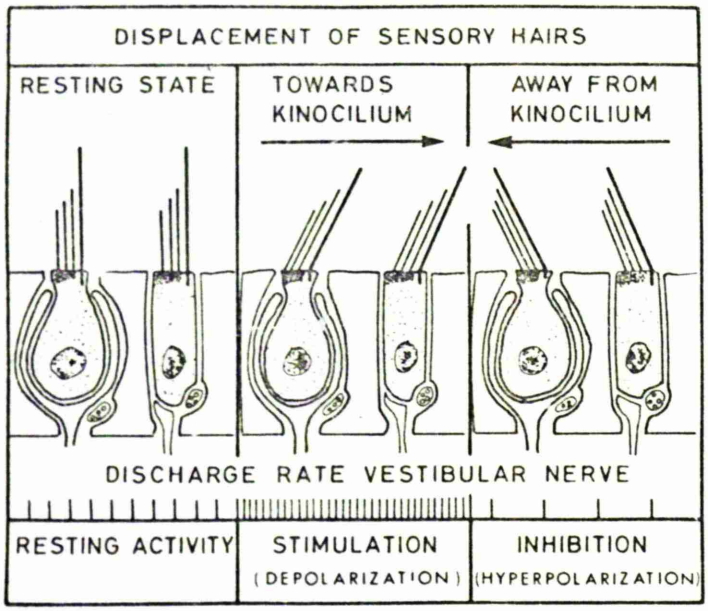
Δ = directional momentum per unit angle.

x = angular deviation of cupula (endolymph).

$\dot{x}$ = angular velocity of cupula (endolymph).

$\ddot{x}$ = angular acceleration of cupula (endolymph).

From this it may be determined that the rate of cupular restoration, which will be termed the time constant of decay or slope value, is given by the ratio π/Δ. This function is frequently used in the present study, as a single expression, to describe and compare the pattern of cupular behaviour in different experimental situations; similarly, the peak initial slow phase velocity of evoked nystagmus is the other expression which will be commonly used, and is designated ωt_o. The practical derivation of both these expressions is simple, and may be found in Appendix 1B.



Electrical discharge rate of the hair cells as a function of displacement of the sensory hairs.

Figure 2.5

Diagram illustrating how the resting activity of the sensory cells in the crista is altered depending on the direction of displacement of the kinocilia (cupula).

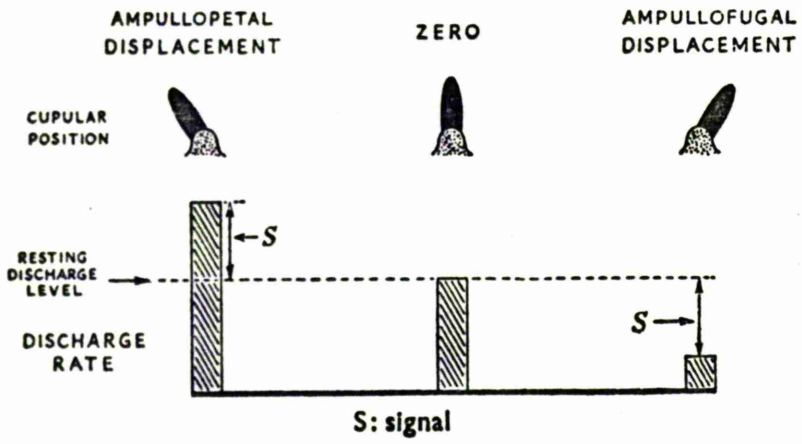


Figure 2.6

Further diagram illustrating how discharge from the cupular end organ depends on the direction of displacement of the cupula, to or from the utricular ampulla.

The hair cells of the cupula are not inactive in the resting state, but give off a continuous resting discharge. On stimulation in response to an angular acceleration, this 'base line' discharge alters, being increased when cupular deflection is towards the kinocilia (or utricular ampulla - ampullopetal displacement), and decreased when it is away from the kinocilia (or utricular ampulla - ampulla fugal displacement), Figs 2.5 and 2.6.

In considering the effects of linear acceleration on responses to angular motion it is relevant to discuss whether the canals, or parts of them, are gravity sensitive. This has been mentioned in Part 1, but nothing said on the important question of the specific gravity of these structures. Here the present position with respect to man is unsatisfactory in that these properties do not seem to have been determined - probably because of the extreme difficulty of obtaining measurable quantities (Money 1968, personal communication). Money seems to be the only worker who has, as yet unsuccessfully, attempted to do so, but as he notes in relation to the cupula "It behaves as a water filled skin, which simply collapses if you attempt to insert a pipette". It does not have the firm gelatinous structure commonly attributed to it, but rather that of a thin elongated balloon containing watery fluid of

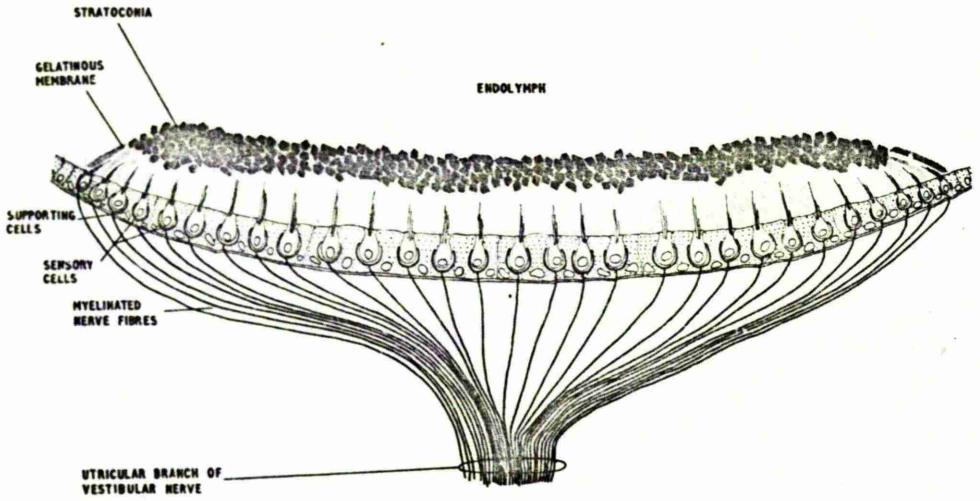


Figure 2.7

Diagram of a vertical section through a utricular macula. The hairs of the sensory cells pass into an overlying gelatinous membrane. In the upper part are numerous calcium carbonate crystals (statoconia) which increase the density so that the otolithic plaque will respond to gravity and other linear accelerations. The sensory cells are thought to be stimulated by shearing forces as the plaque shifts from side to side.

comparable viscosity to endolymph. From this it would seem unlikely that the cupula differs appreciably in density from the endolymph, and therefore that it would be gravity sensitive under normal circumstances.

Similarly, specific gravity measurements of endolymph and perilymph do not seem to have been made. The old observations of Dähnhardt (1869) that the "solid constituents" of endolymph and perilymph were 1.5% and 2.1% respectively, implied that the density of endolymph was less than that of perilymph. More recently Kajeda (1930), in the shark, found the density of endolymph was 1.024 and perilymph 1.0200. In pigeons, Money (1966) found the specific gravity of endolymph and perilymph was 1.0033 and 1.0022 respectively. Thus there appears to be little difference between the two fluids, and it may be proposed from these figures that the density of the membranous canal and contained endolymph is likely to be a little greater than that of the perilymph which surrounds it (Benson and Bodin 1966).

The otolith organs comprise the utricle and saccule, the sensory cells of which are grouped together in the form of plates or maculae (Fig 2.7), lying in a dilatation of the vestibular cavity, also known as the ampulla. Each is invested in a gelatinous membrane which has a higher density than the

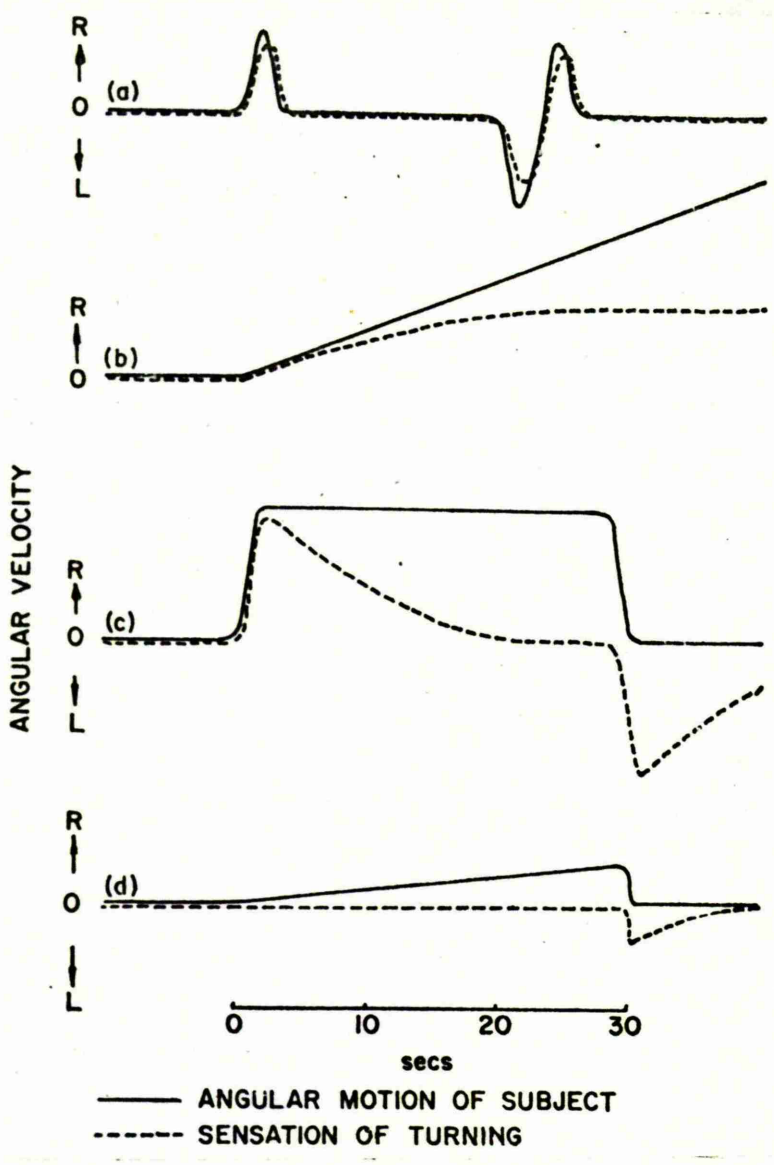


Figure 2.8

Sensations of turning associated with different patterns of angular motion.

(a) Brief short movements (less than 3 sec. duration), acceleration being followed by deceleration. Sensations correspond closely to the physical stimulus.

(b) Constant angular acceleration evokes a sensation of turning at steady velocity once deflected cupular equilibrium conditions have been reached.

(c) If steady velocity is maintained, turning sensations decay exponentially and eventually disappear. On sudden deceleration, false sensations of turning in the opposite direction are engendered which decay with a similar exponential time course to that evoked by the initial acceleration.

(d) Sub-threshold acceleration does not evoke a sensation of turning. On stopping at a rate above threshold a false sensation is evoked which decays exponentially.

endolymph due to calcareous particles or otoliths embedded in it. The sensory cells are basically of two types similar to those found in the crista ampullaris. the paired utricular maculae lie approximately in a horizontal plane when the head is vertical, while the macular plates of the soccule lie in a vertical plane and face laterally.

Electrophysiological studies have shown that the macular receptors respond only to linear acceleration, while present evidence suggests that contrary to expectation they are not sluggish but 'quick responding' end-organs (Personal observation). The utricular and saccular maculae could be expected to respond to linear accelerations in the three orthogonal planes, but precise knowledge of their functional organisation and the mechanism of stimulation of these receptors awaits further research (Lowenstein, 1956; Gemandt, 1959).

The function of the vestibular apparatus is thus that of a specialised organ of equilibrium. In man it lacks the autonomy observed in more primitive animals, e.g. fish, reptiles, but it still exercises powerful control over somatic musculature. Movements of the head or body sufficient to stimulate the vestibular receptors evoke three responses: sensations of movement which allow changes of position to be perceived (Fig 2.8), and become accessible to voluntary control if desired, although

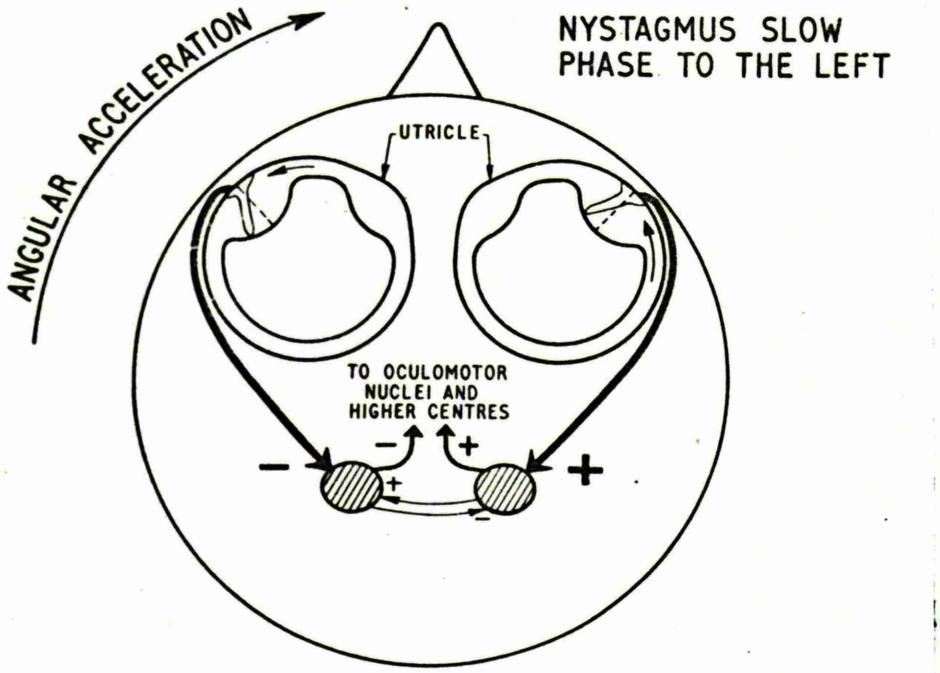


Figure 2.9

Greatly simplified diagram of some vestibulo-ocular connections. As the head rotates in a clockwise direction, endolymph flow and cupular deflection in the right lateral canal is ampullopetal (stimulatory (+)) and correspondingly ampullofugal (inhibitory (-)) in the opposite canal. Afferent signals pass via the vestibular nerve and nuclei, where there is interaction between the two sides, to the oculomotor centres. Compensatory lateral nystagmus with slow phase to the left is evoked.

regulation of equilibrium is normally an involuntary mechanism organised at a low level in the C.N.S; compensatory changes in somatic muscle tone to maintain normal or desired posture; concomitant compensatory eye-movements (nystagmus) which serve to stabilise the retinal image (vestibula-ocular reflex arc). The present study is concerned particularly with the first and the third of these functions.

Vestibular pathways within the central nervous system parallel the wide distribution of vestibular reflexes. The vestibular branch of the 8th cranial nerve carries afferent fibres from peripheral receptors, via the vestibular ganglion, to the medulla, where they form synaptic connections with neurons of the ipsilateral vestibular nuclei. Outgoing efferent fibres also pass in the vestibular nerve to peripheral end-organs, but the complex central connections and functional role of these are not well understood.

There are four principal vestibular nuclei, but their fibre connections are uncertain; it is a convenient simplification to consider them as one functional unit from which ascending and descending tracts originate. The more important of these pass in the medial longitudinal bundle to the oculomotor nuclei (Fig 2.9) and downwards as the vestibulo-spinal tract to segmental motor neurones, and to the nodulus

and flocculus of the cerebellum. Interconnecting tracts pass between the vestibular nuclei via the reticular formation of the mid brain, and from there also to the vagus and glossopharyngeal nuclei, where they presumably mediate the autonomic reflexes associated with vestibular stimulation (pallor, sweating, salivation, nausea, tachycardia).

There is clinical and physiological evidence of vestibular cortical representation in the temporal lobe, but vestibulo-cortical pathways have not been demonstrated anatomically.

More detail descriptions of the vestibular pathways may be found in standard neuroanatomical texts, e.g. (Brodal et al (1962).

PART 3

GENERAL EXPERIMENTAL PROCEDURES AND TECHNIQUES

PART 3

GENERAL EXPERIMENTAL PROCEDURES AND TECHNIQUES

1. Definition of Terms

Certain expressions which may be unfamiliar or ambiguous will be used in this thesis with the specific meanings described below:

(a) General. In the experiments comprising the present study (elaborated in Parts 4 and 5), human subjects were exposed to a number of constant velocity rotations about various body axes, each procedure commencing and terminating with an angular acceleration in the plane of rotation, while evoked vestibular responses were recorded.

For the purpose of describing the planes in which these acceleration stimuli were applied in relation to the subject's body, standard anatomical nomenclature (Birmingham Revision of the Basle Nomina Anatomica) has been used: any plane parallel to the median plane (which divides skull and body vertically into right and left halves) is sagittal. Vertical planes perpendicular to the median plane are coronal. Any plane orthogonal

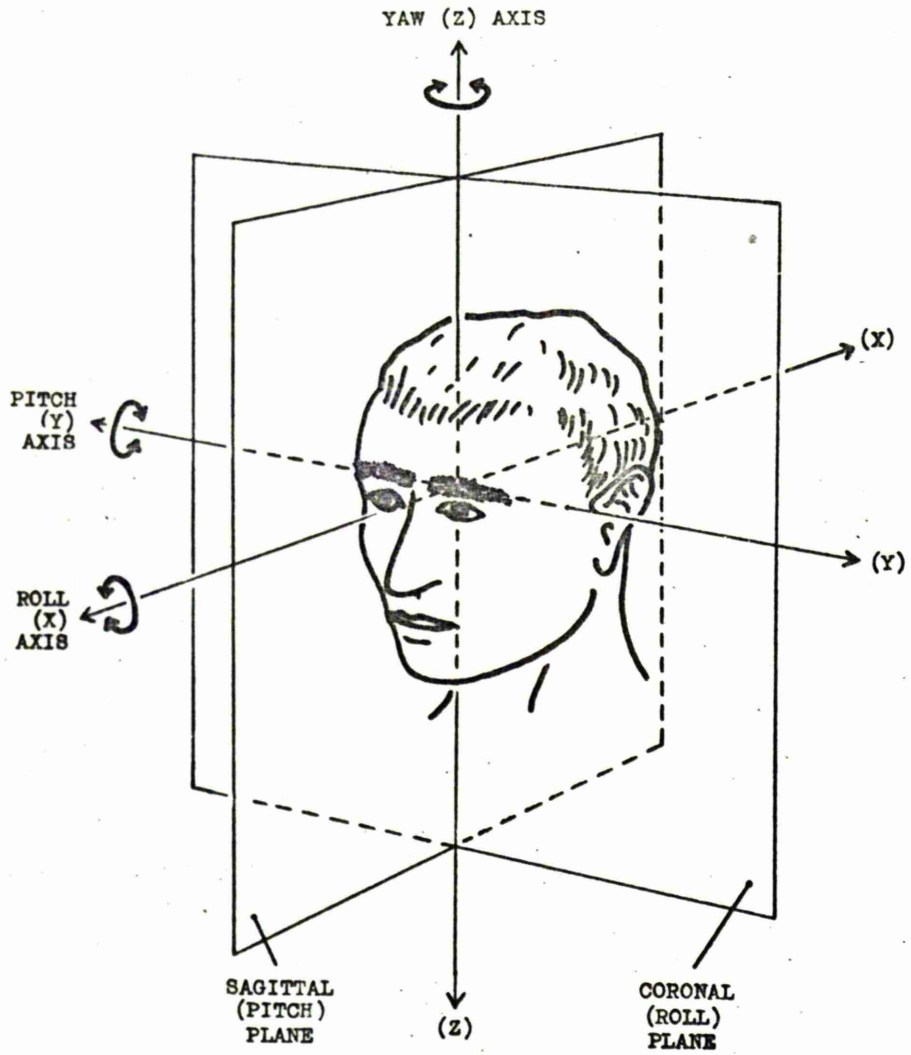


Figure 3.1

Diagram illustrating standard aero-space nomenclature for axes and planes of rotation with respect to the subjects head.

both to the sagittal and coronal planes is transverse.

Vestibular responses which occurred during rotation will be termed per-rotational, those following rotation post-rotational. The direction of nystagmus, whether per- or post-rotation, is taken to be that of the slow phase (vestibular) component.

(b) Rotation axis terminology. For whole body rotation, axes and planes of rotation may be referred either to the head and body (subject-orientated), or to the earth's gravitational field (gravity-orientated). Both systems are used in this study.

For subject-orientated reference, standard aero-space terminology for orthogonal body axes (Gell, 1961) defined with respect to the head, and rotation about these axes, is used (Fig 3.1). In this coordinate system the axes are labelled x, y and z, as indicated. In addition, each is named according to the angular movement experienced by a pilot during rotation of his aircraft about that particular axis, the nomenclature (Fig 3.1) being similar to that for the more familiar motions of a ship in rough weather, namely: yaw - rotation about a cephalo-caudal (z) axis (angular acceleration in a transverse body/skull plane); pitch - rotation about a

lateral (y) axis perpendicular to the long axis of the body (angular acceleration in the sagittal plane); roll - rotation about an antero-posterior (x) axis perpendicular to the longitudinal body axis (angular acceleration in coronal plane of the body).

For gravity-orientated reference, the terms vertical and horizontal are used with their normal meaning, that is, axes of rotation which are parallel or perpendicular to the prevailing gravitational vertical respectively.

Frequently, however, both reference systems will be used in the description of an experimental procedure - the plane of angular acceleration through the skull being defined with respect to the subject, and the orientation of the rotation axis specified in relation to the gravitational vertical. For example, a subject may be rotated in yaw with the cephalo-caudal body axis in a vertical or horizontal position; or in pitch or roll with the appropriate axis of rotation (perpendicular to the long axis of the body) again either vertical or horizontal.

To clarify possible confusion, these situations will be illustrated diagrammatically later, under the particular experiments in which they were used.

2. Vestibular Stimulation: Method Employed and Pattern of 'Classical' Responses

There are a number of ways in which the ampullary receptors of the semicircular canals may be stimulated in intact human subjects - by angular acceleration, thermal (caloric) stimuli, or electric current. Each has its uses and drawbacks, though the latter lacks the specificity desirable for precision application (Camis, 1930) either in research or clinical fields. The caloric test (Fitzgerald and Hallpike, 1942) is now that most widely used for clinical purposes, but as the semicircular canals are physiologically angular accelerometers, it is both logical and advantageous to use rotational stimuli in a study in which ~~the nature of transduction,~~ stimulus-response relationships, and possible interaction effects within the vestibular system will all be considered.

A great variety of rotational procedures may be employed (see Arslan, 1955), but those used today for clinical test purposes are essentially modifications of the familiar Bárány (1907a and b) chair procedure, based on the work of Buys (1937) and Van Egmond, Groen and Jongkees (1948, 1949). In these techniques (well reviewed e.g. by Cawthorne, Dix, Hallpike and Hood, 1956; Howard and Templeton, 1966) rotation is carried

out with the subject seated upright on a chair which revolves about a vertical axis, and post-rotational vestibular responses (nystagmus and turning sensations) produced by a rapid stopping stimulus are recorded. In this way only the ampullary receptors of the lateral (horizontal) semicircular canals are stimulated, and the nature of the evoked responses (lateral nystagmus in particular) depicts the 'classical' pattern of vestibular behaviour (i.e. for rotation in yaw about a vertical axis, in so far as the great majority of human studies have been carried out in this way.*)

In the present series of investigations, rotation in yaw about a vertical axis was performed both as a simple screening test for selection of subjects (see 6 below), and also as an integral part of every experiment in order to establish the 'classical' response pattern for each group of subjects, so that this could be used as a 'base line' for comparison with the results obtained in the ensuing experimental situations.

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* Only comparatively recently has attention been paid to human rotation about other (pitch and roll) axes, and the much more complex problem of interpretation, when responses are engendered by concomitant stimulation of the ampullary receptors in both pairs of vertical semicircular canals.

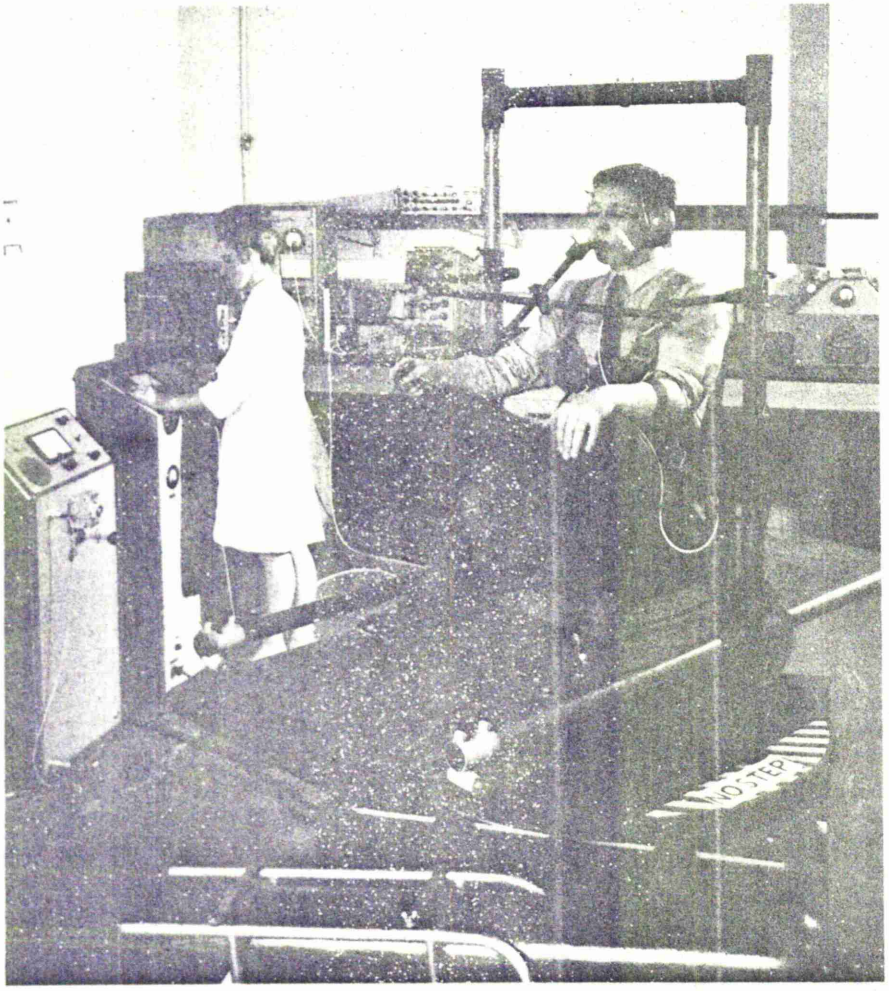


Figure 3.2

Diagram of basic turntable with the subject seated upright for rotation in yaw about a vertical axis. The subject is wearing ear pads, and gripping a dental bite to stabilize the head.

The procedure was carried out in a quiet dark room, with the subject seated upright on a turntable (Fig 3.2) with the eyes closed. Rotation commenced with an impulsive acceleration (5e) to a velocity of 60°/sec, and continued at this speed for one minute, before being terminated by an impulsive deceleration.

Following initial acceleration to constant velocity, compensatory lateral nystagmus develops (Fig 3.3a), i.e. with slow phase component in the opposite direction to the angular motion of the subject, and commences to decay until no longer discernible after about 30 - 40 sec. For quantitative evaluation of eye-movement records, the velocity of each slow phase nystagmic component was calculated (Appendix 1A), and these values plotted against time to give a graphical representation of the pattern of decay of nystagmus. This follows an exponential time course (Fig 3.3c) with an average time constant (Appendix 1B) of about 12 sec. Sensations of turning engendered by the acceleration stimulus decay more rapidly than the nystagmus, and are usually no longer perceptible after about 20 - 30 sec.

On stopping, rapid deceleration from 60°/sec engenders post-rotational lateral nystagmus in the

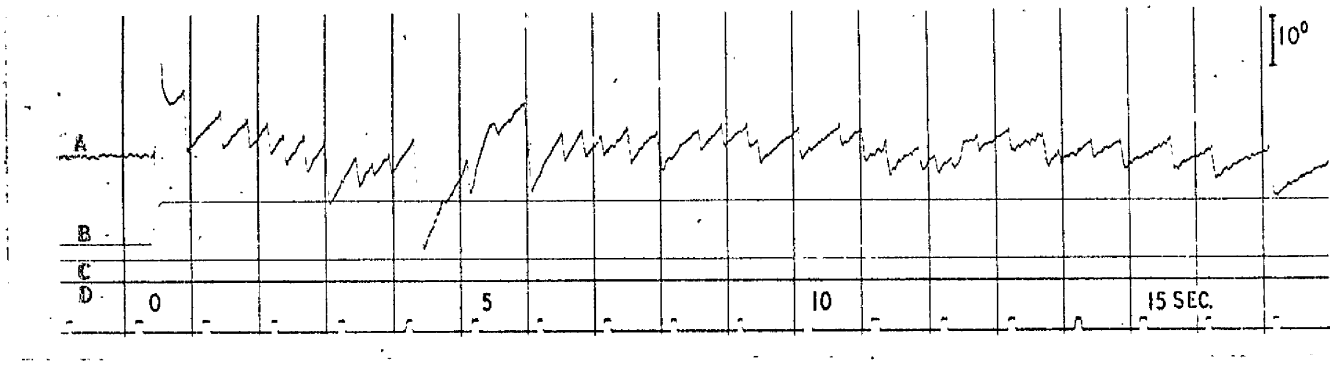


Figure 3.3a

Record of per-rotational lateral nystagmus (A) obtained from a subject following rapid acceleration to a velocity of 60° /sec (B) about a vertical axis in yaw.

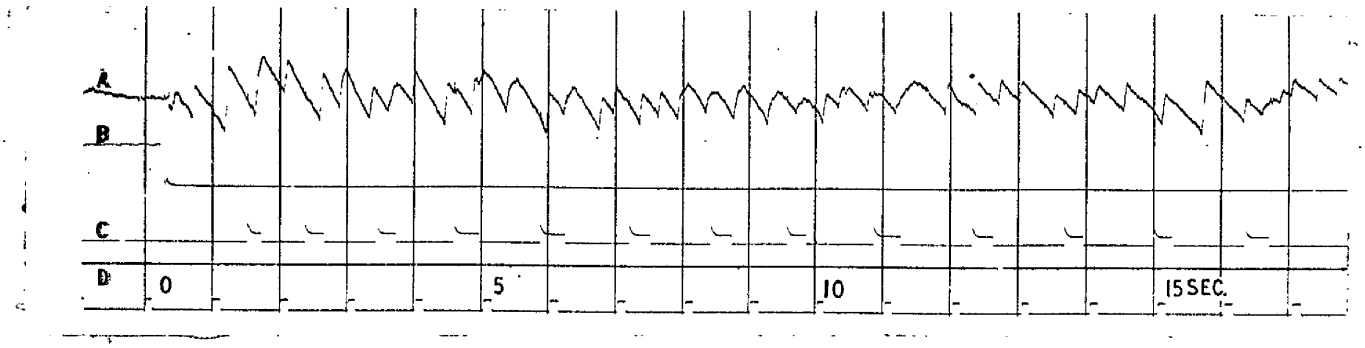


Figure 3.3b

Record of post-rotational lateral nystagmus (A) following rapid deceleration (B) from a velocity of 60° /sec about a vertical axis in yaw. After-sensations of turning are indicated on trace C: the subject pressed a button each time they felt they had rotated through 90°. Note gradually increasing interval indicating decay of illusory sensations.

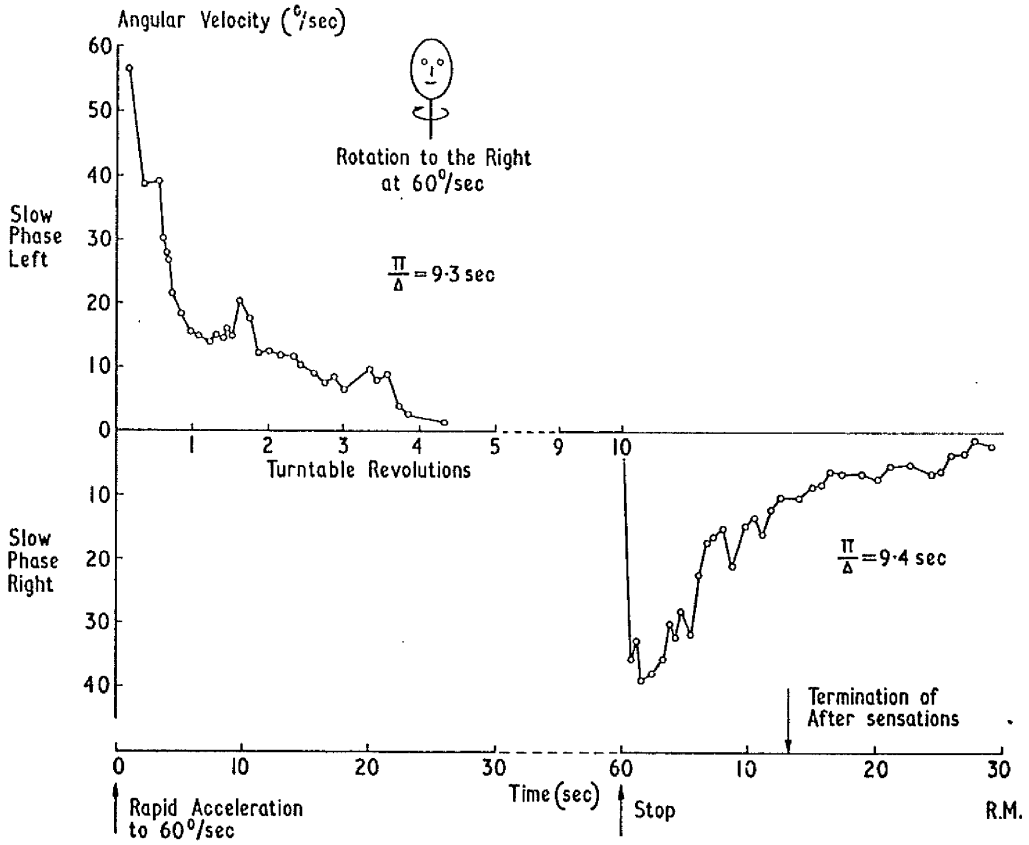


Figure 3.3c

Exponential pattern of decay of velocity of slow phase lateral nystagmus during and after rotation at 60°/sec about a vertical axis in yaw. Ordinate and abscissa scales are linear. Note that per and post rotational time constants of decay (π/Δ) are similar. After-sensations of turning persisted for 13 sec, and nystagmus for almost 30 sec in both situations.

opposite direction (Fig 3.3b), which decays with a similar pattern and time course to that of the per-rotational eye-movements (Fig 3.3c), while after-sensations of turning may again persist for up to 30 sec.

Several factors can influence the pattern of per- and post-rotational responses as outlined above, and these will be considered in greater detail in sub-section (5).

3. Method of Recording Eye-Movements: Electronystagmography (Electrooculography, EOG)

Many methods may be used to record eye-movements, e.g. direct photography (Buys,1909; Ohm,1914; Dohlman,1925; Free and Jones,1959), television techniques, direct reflection from the corneal surface, scleral search coils and other contact lens techniques. Byford (1961) has reviewed the advantages and disadvantages of these methods. The technique of electronystagmography has drawbacks like any other, but it offers many advantages, including practical simplicity and subject acceptability which render it particularly suitable for routine vestibular physiological purposes. It is widely used by most workers in this field today, both with animal and human subjects.

Early publications on electronystagmography first appeared in 1922 (Schott), and much has been written since then.

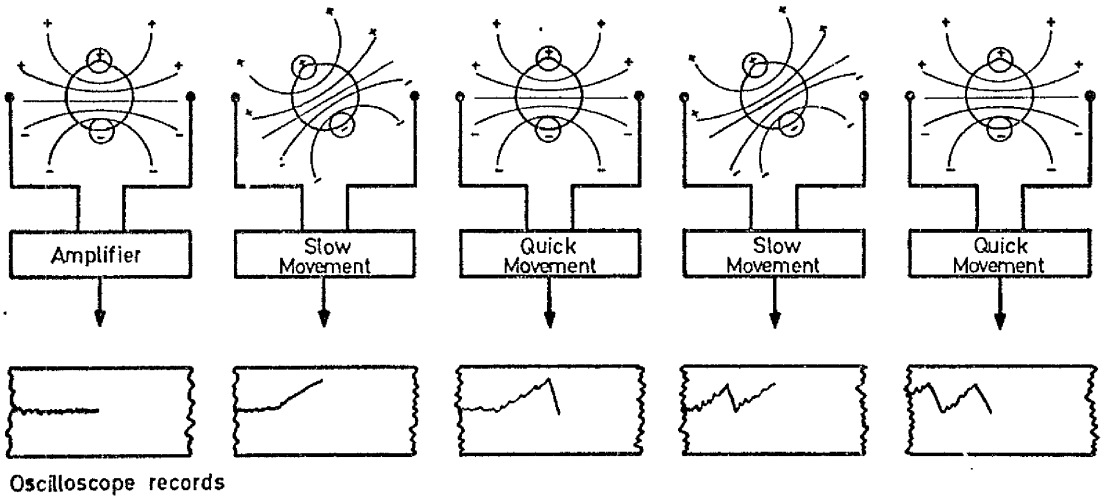


Figure 3.3d

Diagram to illustrate the principle of electronystagmography. Because of its corneo-retinal potential the eyeball acts as an oscillating dipole during nystagmus. Scalp electrodes placed in the plane of movement pick up the changing component of potential. This is suitably amplified, displayed on an oscilloscope, and recorded to give a continuous record - the electroculogram (E.O.G.), as in Figs 3.3a and b.

The method is well reviewed by Bergstedt and Stahle (1956) and Jongkees and Philipszoon (1960), among others.

Nystagmography depends on the existence of a potential across the eyeball, since it is a polarized sphere with the cornea positive and retina negative - the so called cornea-retinal potential, first described by du Bois-Reymond (1849). Thus as the eye moves, provided the cornea translates in space, it functions as a rotating dipole, and electrodes placed on the scalp close to the margins of the orbit will pick up the changing potentials. These can be suitably amplified and recorded to display the eyemovements (Fig 3.3d). Horizontal or vertical eye-movements may be studied in this way, but for obvious reasons not torsional ones (roll) as the axis of polarization is then fixed in space.

Either subcutaneous or surface electrodes may be used, but subject acceptability was paramount in the present study, and E.M.I. rubber suction cup electrodes (Shackle, 1957) proved both highly convenient and successful. These stick to the skin like a child's rubber dart. The only notable point is that simple but meticulous preparation is desirable if the electrodes are to function adequately (Appendix 2). If these requirements are fulfilled, eye deviations down to an amplitude of about 1^{o}

of arc are readily discernible; under average recording conditions the apparatus was set to give a maximum amplitude of about 10° for initial high velocity nystagmus wave forms, and a noise level corresponding to $\frac{1}{2}$° or less, could usually be achieved, though the latter varied considerably with the subject and type of nystagmus being examined (see below).

The electrode input voltage was usually between 50-100 microvolts, i.e. a sensitivity of about 5-10 microvolts/degree, and over this limited range the potential recorded is proportional to the sine of the angle of eye movement. A stable DC amplifier was used, and the frequency response of the recording system was 0 - 60Hz. This ensured that slow drifting or swinging eyemovements lasting for several seconds (e.g. ref. Part 4, section 1) would be accurately recorded, which would not be possible with an AC amplifier due to its short time constant. For this reason, although not as easy to handle as an AC system, DC amplification was preferred because it gives a more accurate reproduction of eye position in circumstances where slow changes from the iso-electric line may occur.

Problem sources, which cause the main difficulty with this system of eye recording are twofold: other biological potentials

picked up by the electrodes, and factors which introduce changes or differences in the cornea-retinal potential itself.

Artifact potentials come from E.M.G. of eye muscles, or other neighbouring muscles, e.g. masseters if the subject is not relaxed, E.E.G. spikes are occasionally seen, eyelid potentials if the subject blinks (the latter are largely avoided with the eyes closed - see below), and potentials due to soft tissue movement as the subject rotates. Factors affecting the quality of electronystagmograms have been reviewed by Dowd (1965). Changes in the cornea-retinal potential on the other hand, may occur depending on ambient illumination, 'arousal' level of the subject, diurnal rhythm and intersubject variations (Byford, 1961). Consequences of these changes were largely removed by conducting experiments in a dark room, with the subject's eyes closed, and recording frequent calibration eyemovements before and after every run in a series (Appendix 1A).

None of these factors therefore presented serious difficulties under the experimental conditions described. Electronystagmography undoubtedly provided the best method for examination of eyemovements in the present study.

4. Quantification of Nystagmus Records

Many indices may be used for the quantitative evaluation of post-rotational nystagmus records (Fig 3.3b), but the following are among those most frequently employed:

(a) Duration of nystagmus, measured as the interval in seconds between cessation of angular deceleration and the last discernible nystagmus beat. The method is one of the most popular and has been widely used over the years both by clinical neuro-otologists and research workers (e.g. Bárány, 1907a; Malan, 1926; Van Egmond, Groen and Jongkees, 1948; Fluur and Mendel, 1962a; Guedry, 1964; Collins, 1969, to mention but a few). Measurement of duration is theoretically a quick and simple procedure, but this convenience in practice is more than off-set by the frequent difficulty encountered in determining the precise 'end-point', and the fact that it is also a particularly labile index (Herlitzka, 1923; Malan, 1926) - see below.

(b) Amplitude ('Intensity') of Nystagmus. (Herlitzka, 1923; Camis, 1930). A cumulative measure of (vertical) displacement of the slow phase nystagmus components. It may be expressed either as the total

slow phase displacement of all nystagmic beats recorded (Gesamtamplitude - Mittermaier, 1954), or more commonly as the sum of slow phase nystagmus displacement during the 60 sec following deceleration of the subject ('nystagmus output', e.g. Correia and Guedry, 1964); that is, the integral of nystagmus angular velocity from $t = 0$ to $t = 60$ sec (a measure which for practical purposes approximates to the integral of nystagmus velocity (ω) from $t = 0$ to ∞, given by the product of initial slow phase velocity (ωt_o °/sec) and the time constant of decay (π/Δ sec).

(c) Frequency. The number of nystagmic beats/unit time (e.g. Aschan, Bergstedt and Stahle, 1956).

(d) Degree. The presence or absence of nystagmus in relation to the direction in which the subject is looking, usually expressed as being of first, second or third degree (e.g. Fischer, 1956).

(e) Rating. A qualitative assessment of overall nystagmic response, including consideration of amplitude, frequency and regularity of beats, usually expressed on a scale of 0 - 4 (e.g. Collins, Guedry and Posner, 1962).

(f) Vector scoring. A diagrammatic plot of the magnitude and direction of the average resultant of

lateral and vertical slow phase velocity vectors for each 2 sec interval (e.g. Lansberg, Guedry and Grabiel, 1964).

(g) Velocity of slow phase nystagmus. Analysis of the pattern of decay of slow phase nystagmus has been used by many investigators in the past (e.g. Lorente de Nó, 1931; Dohlman, 1935; Hallpike and Hood, 1953; Van Egmond and Tolk, 1954; Groen, 1957, to mention but a few), particularly to determine the rate (time constant) of decay of post-rotational nystagmus, which is probably the best available index of cupular behaviour (Benson, 1967). The technique (Appendix 1) is relatively tedious, however, and today is probably less frequently used for research purposes than some of the quicker indices above.

The principal disadvantage of most of these methods is that they are influenced by factors other than the deceleration stimulus. Amplitude, frequency, duration and 'output', for example, are particularly labile in relation to 'arousal' (5c) and habituation (5d), while duration and 'output', as well as initial slow phase velocity, also depend on the magnitude of the stopping stimulus (5e). Indices (a) - (f) above, therefore, though not infrequently used by contemporary investigators, are inherently unsatisfactory if there is an

indefinite 'end-point' or need for qualitative assessment of the nystagmus record. It is considered that they are potentially of limited value due to difficulties in standardizing experimental variables, and must always be interpreted with considerable caution.

The time constant of decay of nystagmus, on the other hand, as a much more stable index (sub-section 4), is less subject to these limitations, and for this reason has been used in the present study as the best available objective measure for the quantitative evaluation of post-rotational nystagmus. The procedure for routine analysis of nystagmus records, using this method, is described in Appendix 1.

5. Factors Influencing the Pattern of Vestibular Responses to Rotational Stimuli

A variety of factors, other than applied acceleration stimuli, may influence the 'common' pattern of per- and post-rotational responses (above), and these therefore received special attention in the planning and conduct of the main experiments:

(a) Other perceptible sensory information. It is essential that other sensory cues to the presence or absence of motion should be minimal or absent. Special care was taken in the design and construction of

rotating apparatus, in addition to other precautions described later, to ensure mechanically smooth noise/vibration-free movement, and firm head fixation.

Visual stimuli are particularly undesirable, and during rotation may produce optokinetic nystagmus (Helmholtz, 1962), which will dominate and distort vestibular induced eye-movements (Dodge, 1923; Wendt, 1951). This can occur even through closed eye-lids, if appreciable differences in the intensity of surrounding illumination are present (personal observation). Following rotation, if the eyes remain open visual fixation will usually rapidly 'damp out' post-rotational nystagmus (Mowrer, 1935; Wendt, 1951; Aschan, Bergstedt and Stahle, 1956; Guedry, Collins and Sheffey, 1961; Collins, 1967), particularly in the yaw and pitch planes (Melvill Jones, 1963) with which the present studies were primarily concerned. Unnecessary exposure to light during the course of an experiment (e.g. between 'runs') may also affect the corneo-retinal potential of the eye, sufficient to influence the accuracy and consistency of nystagmus records obtained by electronystagmography (sub-section 3); frequent calibration eye-movements were therefore recorded, in the manner described later, to mitigate possible errors arising in this way.

Directional (environmental) noise cues were avoided by conducting experiments in a quiet room, and providing the subjects with ear pads.

(b) Direction of rotation. Vestibular responses to equal angular acceleration stimuli are usually symmetrical irrespective of the direction of rotation (Malan, 1926; Aschan, 1954; Fischer, 1956; Howard and Templeton, 1966), and indeed an appreciable difference between responses in the two directions (directional preponderance; vestibular asymmetry) has long been considered pathological, even though the clinical significance of this finding has been disputed (Anderson, Jepson and Kristiansen, 1956).

Recent studies, however, throw considerable doubt on this interpretation (apart from the few well known clinical syndromes mainly attributable to comparatively gross unilateral impairment of peripheral vestibular function), and Benson (1967) in particular has shown that following rotation in yaw about a vertical axis, some 15% of 'normal' individuals (i.e. without either symptoms or clinical evidence of vestibular disease) show a significant difference in after-sensation measures and/or pattern of nystagmus decay (4g) for the two directions of rotation. Nevertheless, directional preponderance is

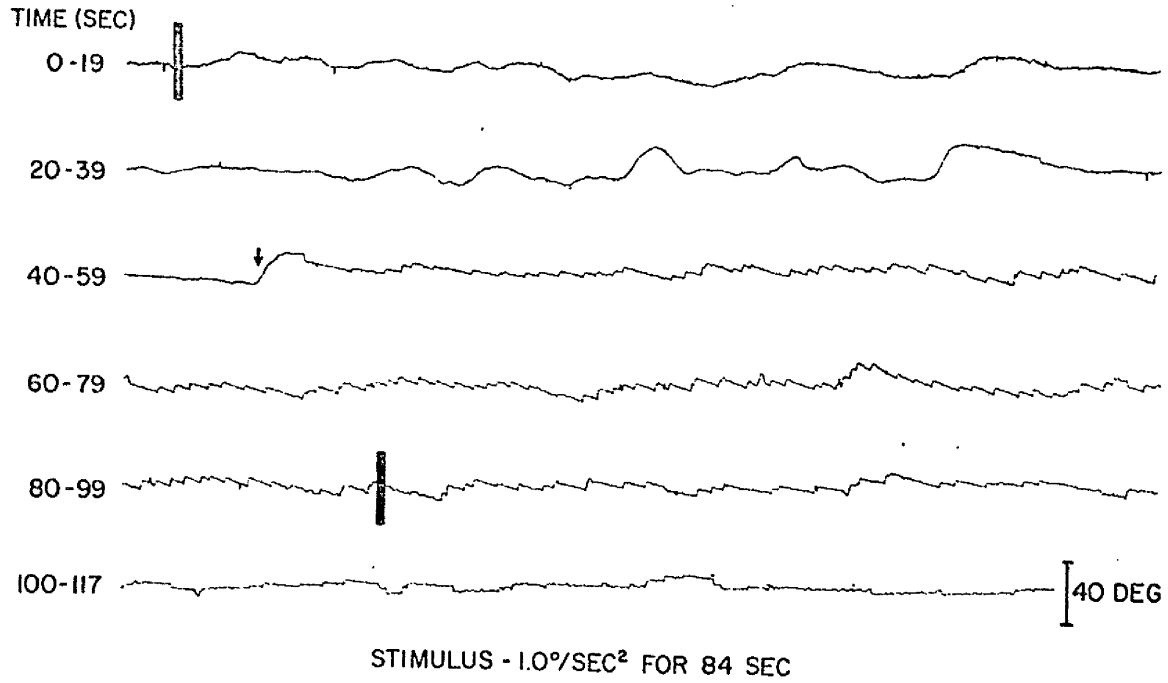


Figure 3.4a

Effect of arousal on lateral eye-movements produced by a $1^{\circ}/sec^{2}$ acceleration about a vertical axis in yaw. Acceleration was applied during the period between the heavy black lines. Initially the subject was mentally relaxed. After 43 sec they were instructed to commence and continue simple mental arithmetic (arrow). This evoked well marked nystagmus, in contrast to the slow swinging eye-movements present previously, which persisted during acceleration and for about 20 sec of constant velocity rotation.

undesirable for experimental purposes, and individuals who showed such asymmetry on initial screening (sub-section 6) were not used as subjects.

The order in which rotation in different directions is carried out is also important, as this may influence the possible effects of 'habituation' (5d).

(c) State of 'arousal' of the subject. The degree of mental alertness ('arousal') of a subject can significantly influence vestibular responses to angular acceleration (Guedry, 1965), although the consequences of differences in 'arousal level', in practice, depend appreciably on the index of vestibular function being measured. The main objective indices which may be used for this purpose have been described above, but among those most frequently employed, nystagmus amplitude, duration and 'output', are all particularly labile in this respect (Bach, 1894; Mowrer, 1934a; Collins, 1963; Crampton, 1964). A given acceleration stimulus, for example, may evoke minimal (or absent) eye-movements in a relaxed subject (e.g. attending only to their sensations of turning), but a well defined nystagmus if their mental activity is increased (heightened arousal) by performing a task such as simple mental arithmetic (Fig 3.4a) (Collins, Crampton and Posner, 1961;

Collins, Guedry and Posner, 1962; Dowd, 1965). The rate (time constant) of decay of slow phase nystagmus velocity (4g), on the other hand, is a much more stable index, and appears to alter very little (if at all) in relation to changes in 'arousal level', at least over the limited (though practically useful) range between attending to sensations and performing mental arithmetic (Benson and Bodin, unpublished observations), encountered in most of the experiments to be described.

In certain circumstances (though not directly applicable to the present study) there is some evidence to suggest that arousal may slightly influence the rate of nystagmus decay (Benson, Goorney and Reason, 1966). Nevertheless, time constant of decay is still almost certainly the most stable objective index of vestibular behaviour, especially when uniform levels of arousal cannot be presumed even during the course of a single experiment, let alone among different subjects, and for this reason has been used throughout for the quantitative evaluation of nystagmus in the present study.

(d) Repetition of acceleration stimuli. Effects attributable to 'habituation' ("the gradual diminution

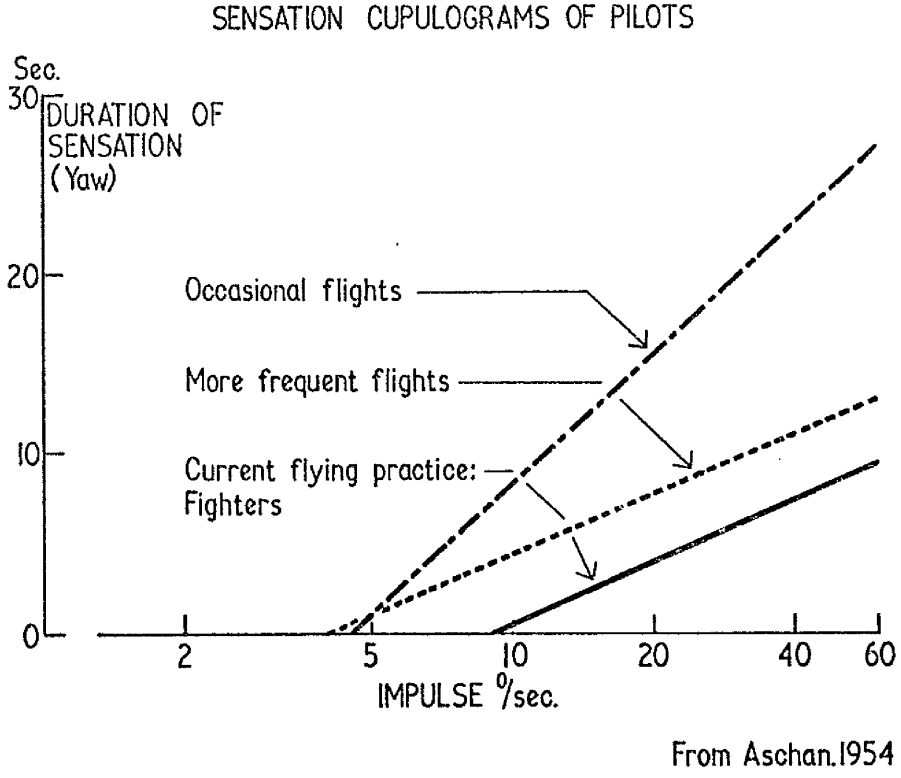


Figure 3.4b

Sensation cupulograms of pilots illustrating habituation. Idealized curves taken for groups of pilots (as indicated) who were rotated about a vertical axis in yaw, and the duration of after-sensations (linear ordinate) plotted for different stopping stimuli (log impulse applied) on abscissa. Flat curves (shorter after-sensations for a given stimulus) or displacement to the right (high 'thresholds') indicate habituation. Pilots in current practice (regular exposure to vestibular stimuli) show the greatest habituation.

of responses to repeated stimulation" - Glazer, 1966) are likely to arise if successive rotational procedures are performed on the same subject, for it is well established that exposure to repeated angular accelerations causes a progressive reduction of vestibular responses (Dodge, 1923a; Mowrer, 1934; Groen, 1957; Guedry and Grabiel, 1962; Collins, 1964; Brown and Crampton, 1966; Brand, 1968).

The consequences of habituation , however, differ appreciably depending on the index of vestibular behaviour being measured. Subjective responses (duration and nature of sensations of turning, e.g. Fig 3.4b) habituate more rapidly than nystagmus (Guedry, Collins and Sheffey, 1961; Forssman, Henriksson and Dolowitz, 1963), while objective indices of nystagmus (subsection 4) also vary appreciably in the extent to which they are influenced by habituation: nystagmus output (Guedry, 1965; Brown and Crampton, 1966; Brown, 1967), duration of nystagmus and the number of nystagmic beats (Collins and Updegraff, 1965), for example, being particularly affected. Few investigations have specifically examined the effect of habituation on the rate of decay of nystagmus slow phase velocity, though under conditions somewhat different from those in the experiments to be

described, Brand (1968) has shown some evidence of reduction in time constant of post-rotational nystagmus, with repetition, over a period of several days. Nevertheless, on balance, available evidence would seem to support personal impressions that for a limited number of rotations, such as used in the present studies, the time constant of decay probably changes less with repetition of acceleration stimuli than other indices (Groen, 1957; Benson, 1962, 1964).

The order of direction in which successive angular accelerations are applied is also important, since vestibular habituation is usually directionally specific (Dodge, 1923a; Holsopple, 1923a); that is, habituation in one direction will generally transfer cumulatively to other stimuli in the same, though not in the opposite direction (Henriksson, Kohut and Fernandez, 1961; Crampton, 1962a; Fernandez and Schmidt, 1962a and b; Guedry, 1965).

It has been suggested that lowering of 'arousal' may be responsible for vestibular habituation (Lidvall, 1962; Howard and Templeton, 1966). Nystagmus elicited by repetitive stimulation, for example, shows a smaller reduction if arousal is maintained by a suitable

mental task during the course of the experiment (Collins, 1964). The hypothesis is difficult to substantiate, however, as it rests solely on studies in which indices particularly susceptible to changes in 'arousal' (e.g. duration and 'output' of nystagmus) were used (Wendt, 1950, 1951; Bender, 1955; Guedry and Lauver, 1961; Collins and Guedry, 1962; Guedry and Turnipseed, 1964), so that true habituation , attributable to repetition of stimuli only, could not readily be distinguished from 'attenuation' of responses associated with concomitant decline in arousal as the experiments progressed. Furthermore, increased arousal , following repeated stimulation, fails to restore post-rotational nystagmus to its initial level (Crampton and Schwam, 1961), so that habituation would seem unlikely to be mediated solely by reduction of arousal . In addition, nystagmus time constant of decay, which is relatively stable in relation to 'arousal level' (see above), also seems to show little evidence of change with repetition of acceleration stimuli, at least over the range of rotation procedures encountered in the experiments constituting the present study (personal observations).

Vestibular habituation is well summarized by Howard and Templeton (1966), who conclude that it is

probably a form of learning. But whatever its cause, and this is likely to be complex, due allowance must be made for the possibility of its occurrence, in the planning and conduct of any repetitive rotational procedure (sub-section 7), particularly by suitable choice of a balanced random design for the experimental variables.

(e) Nature of the acceleration stimulus. Vestibular stimulation depends on the magnitude of acceleration, as well as the time for which it is applied. Long acting accelerations are rare in daily life, however, and stimuli associated with normal head movements are usually of short duration in comparison with the time constant of the canal system. In these circumstances, evoked responses are related to the magnitude of the velocity change rather than that of the acceleration, and for short duration stimuli (less than about 3 sec) the product of acceleration ($^{o}/sec^{2}$) and time (sec) for which it acts remains relatively constant in a given individual (Groen and Jongkees, 1948). For rapid accelerations, therefore (to or from stationary in less than about 0.5 sec, as employed in the main experiments described later), the magnitude of velocity of rotation is related to the impulse applied to the end-organ, and provides a convenient index for the comparison of stimuli to the

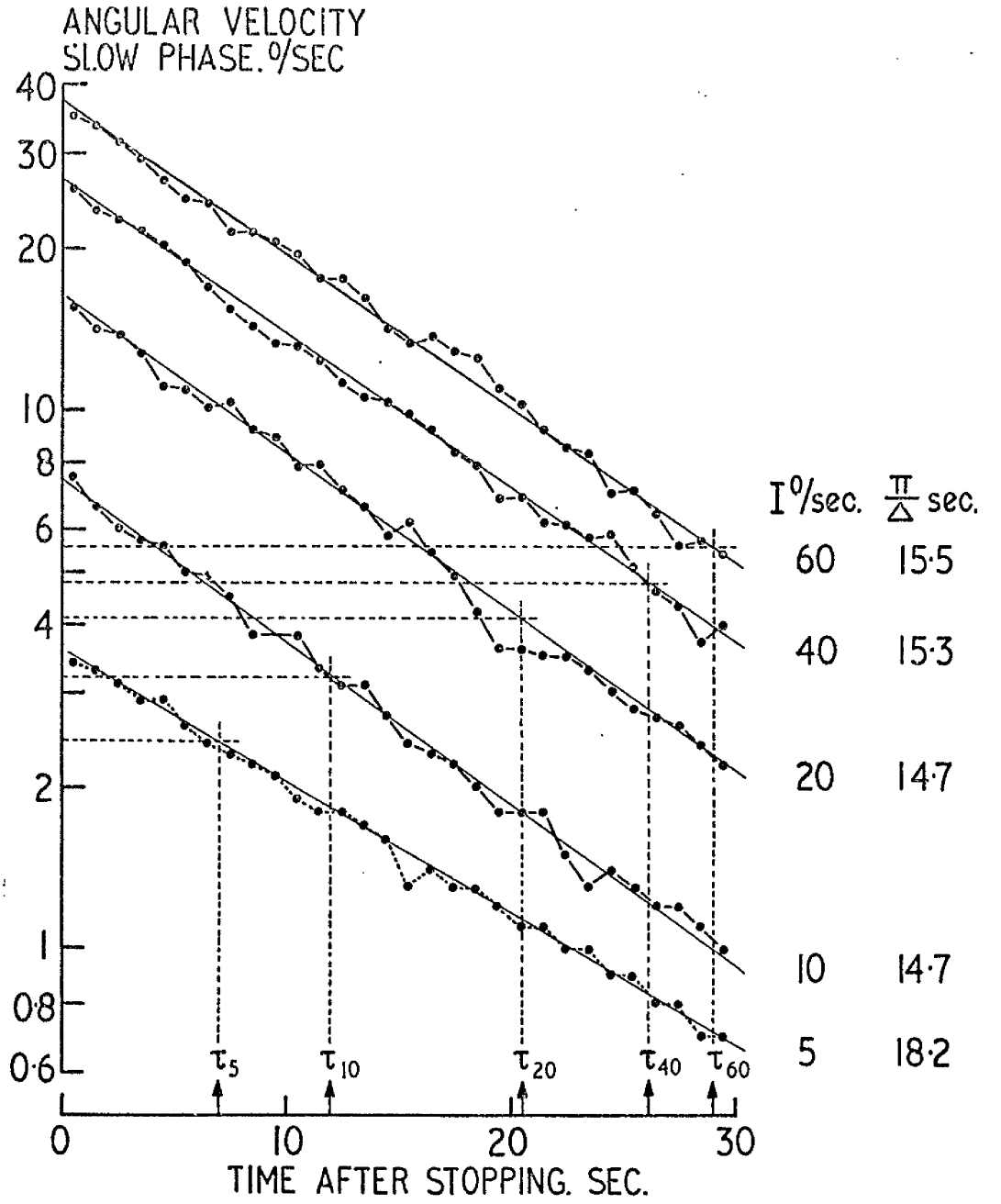


Figure 3.5

Pattern of decay of slow phase velocity (on logarithmic ordinate scale) of post-rotational lateral nystagmus for five different stopping impulses (I). Except at the slowest speed (where it was difficult to obtain sufficient data) the rates of decay (π/Δ) did not differ appreciably. The graphs confirm theoretical expectation that rate of decay is not a function of angular deviation, but peak initial slow phase angular velocity is. (From Benson, 1967).

canal receptors. A rapid deceleration from 60° or 40°/sec, for example, can be expressed as a 60° or 40°/sec stopping stimulus (impulse), and this terminology is used in the present study.

Following such a stimulus, most indices of vestibular response are related to the magnitude (i.e. velocity of rotation) of the impulse applied. Duration of after-sensations, initial slow phase nystagmus velocity (ω_{t_o}), nystagmus duration and 'output', for example, all depend on the impulse applied, and decrease as this is reduced. The time constant of decay of post-rotational nystagmus, however, is essentially independent of the magnitude of the stopping impulse (Fig 3.5) (Cawthorne, Dix, Hallpike and Hood, 1956; Benson, 1967).

6. Selection of Subjects

The subjects used for the main experiments in this study were chosen from service and civilian personnel, of either sex, on the staff of the R.A.F. Institute of Aviation Medicine, usually in the age group 18 - 30 years, and without clinical evidence of aural disease or abnormal vestibular function. Personnel engaged on aircrew duties were not selected, however, because of

possible modification of their vestibular responses through habituation (Fig 3.4b). Prior to selection, each subject underwent a short rotation test seated upright on a turntable (2 above), to allow post-rotational lateral nystagmus to be assessed. Those who showed poor quality nystagmus, spontaneous nystagmus, or significant vestibular asymmetry (5b) were rejected. In general, a different group of subjects was used for each experiment, but when a given individual was asked to participate in more than one procedure, an interval of at least several months commonly elapsed between successive experiments.

7. General Scope and Conduct of Present Investigation

The broad purpose of this study, as initially conceived, was to investigate vestibular responses to angular stimuli about each of the three orthogonal body axes (yaw, pitch and roll) in turn, both during and after rotation, and to compare the pattern of responses when each rotation axis was vertical with those obtained when it was horizontal.

As the project progressed, however, additions and modifications to this basic plan were introduced in the light of results already obtained. In particular, a number of experiments were included in which, following

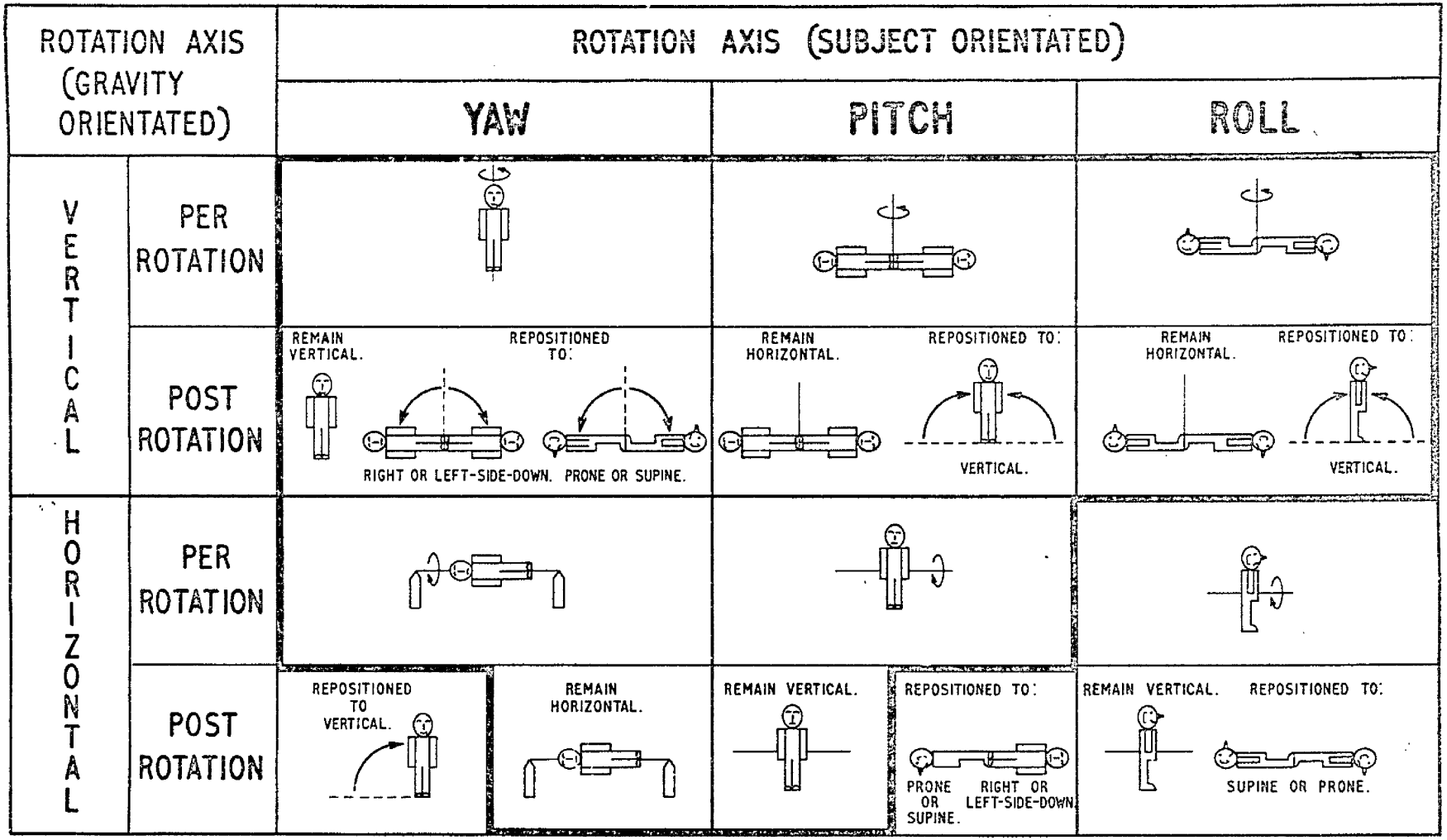


Figure 3.6

Summary diagram illustrating the main experimental procedures comprising the present study. Each is elaborated in detail later, under the appropriate section, with photographs and diagrams to clarify the methods employed. The two left vertical and top horizontal columns show the main variables which determined the number of possible experimental situations, viz the rotation axis with respect to the earth (gravity orientated) may be vertical or horizontal; for each of these positions subjects may be rotated either in yaw, pitch or roll; evoked responses may be recorded either per and/or post rotational, and this may be done with the subject in the same position occupied during rotation, or following a repositioning manoeuvre through 90° with respect to gravity vertical. The diagram shows 18 main possibilities, but for technical reasons only those within the heavy line were carried out.

rotation about different body axes, the subjects were tilted out of the plane of rotation (usually through 90°) immediately they ceased turning, so that responses engendered by an angular stimulus in one plane could be examined after the subject had been moved to a different position with respect to the gravitational vertical (Part 5, sections 3 - 6).

The introduction of these modifications considerably increased the potential scope of the study, if it was to be comprehensive and include rotation about each of the three axes (both when horizontal and vertical, with and without repositioning manoeuvres), but for technical reasons some of these procedures have not been carried out. For clarity, therefore, and to summarize the main content of this study, the various possible experimental combinations are illustrated diagrammatically in Fig 3.6, and those which have been carried out are distinguished from those which have not.

In the conduct of the experiments, a number of basic features were common to all. Each experiment was performed in a quiet, dark room, with the subjects' eyes lightly closed throughout. Turning was initiated either by a slow ($1°/sec^2$) or impulsive ($300°/sec^2$) angular acceleration, to a constant velocity (usually $60°/sec$),

and was carried out both in the clockwise and counter-clockwise direction. In all experiments rotation at constant velocity continued for not less than one minute, before the subject was brought to rest by an impulsive deceleration stimulus ($300^{\circ}/sec^2$).

Per-rotational responses were examined in some experiments (Part 4), and after-responses recorded in every experiment. Records of post-rotational eye-movements were obtained for up to 40 sec, and while these were being recorded subjects were usually instructed to concentrate on their after-sensations of turning, and to press a signalling key when these could no longer be discerned; in some experiments, however, they were asked instead to perform mental arithmetic as an arousal task (5c) to increase the 'nystagmus output'. Descriptions of the nature of after-sensations, as well as measurements of their duration, were also obtained in the majority of experiments.

Most of the experiments involved frequent repetition of essentially similar (though alternating in direction) patterns of angular motion, and to minimise possible effects due to habituation (5d), the number of experimental variables was kept as small as possible, while particular attention was paid to the choice of a

balanced random design for each group of rotation procedures, standardization of environmental conditions, and the nature of preliminary explanation and instructions given to the subjects.

8. Analysis of Results

On the completion of each experiment, subjects were asked to describe the nature of their sensations associated with the various procedures, initially 'un-prompted', and then in answer to specific questions. Special attention was paid to the incidence of discomfort, 'stomach awareness' and nausea. These comments were tabulated and compared. The measurements of duration of after-sensations were averaged for each procedure, and mean values for the different experimental situations determined.

The methods used for the analysis of per-rotational eye-movements will be described in detail later (Part 4, section 1). Quantitative evaluation of post-rotational nystagmus was carried out by determining both the initial slow phase velocity of nystagmus, and the time constant of the ensuing exponential decay of slow phase nystagmus velocity (Appendix 1); the reasons for choosing time constant of decay of slow phase nystagmus as

the best objective index of post-rotational vestibular behaviour have already been indicated (sub-sections 4 and 5).

Subjective and objective response measures were compared respectively for the various experimental conditions, and the significance of differences assessed both by analysis of variance and by non-parametric statistics (Wilcoxon matched-pairs signed-rank test).

PART 4

PER-ROTATIONAL VESTIBULAR RESPONSES

PART 4

Section 1

Comparison of Vestibular Responses During Rotation in Yaw about Vertical and Horizontal Axes

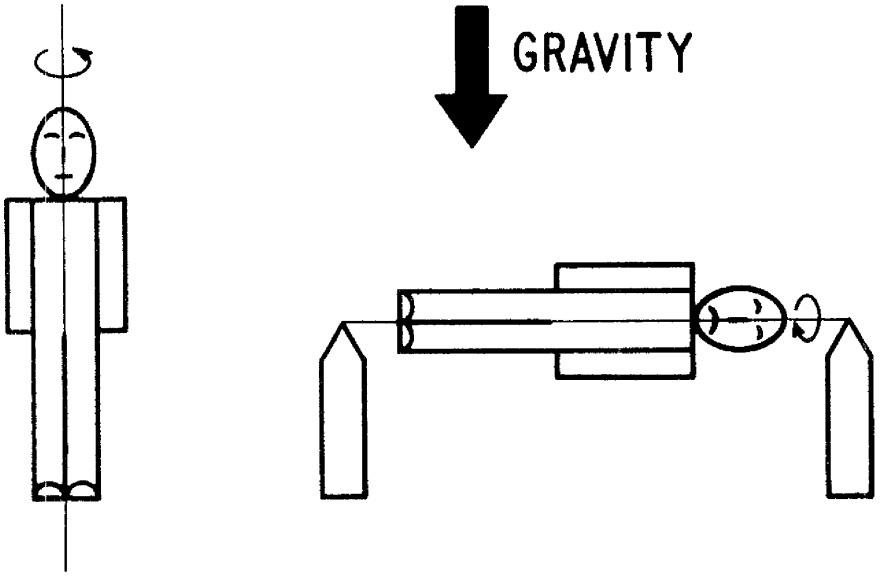


Figure 4.1

Diagram to illustrate the experimental situations for rotation in yaw about a vertical and a horizontal cephalo-caudal axis. The lateral semicircular canals were close to the plane of rotation in both situations, but only horizontal axis rotation involved continuous reorientation of the body relative to gravity.

SECTION 1

COMPARISON OF VESTIBULAR RESPONSES DURING ROTATION IN YAW ABOUT VERTICAL AND HORIZONTAL AXES

Purpose of Experiment

This experiment was performed to investigate the behaviour of the lateral (horizontal) semicircular canals, by comparing the pattern of responses during rotation in yaw about vertical and horizontal axes coincident with the cephalo-caudal axis of the body (Fig 4.1).

In both situations the lateral semicircular canals lay close to the plane of rotation, so that the ampullary receptors of these canals experienced a similar stimulus from the angular acceleration in each situation.

During rotation about the horizontal axis, however, there was continuous reorientation of the subject relative to gravity, as well as rotation of the gravitational vector in the transverse plane of the skull. Neither of these features were present when rotation occurred about the vertical axis. By comparison of the responses in the two situations, therefore, it was possible to assess the contribution of the '1g' linear acceleration vector.

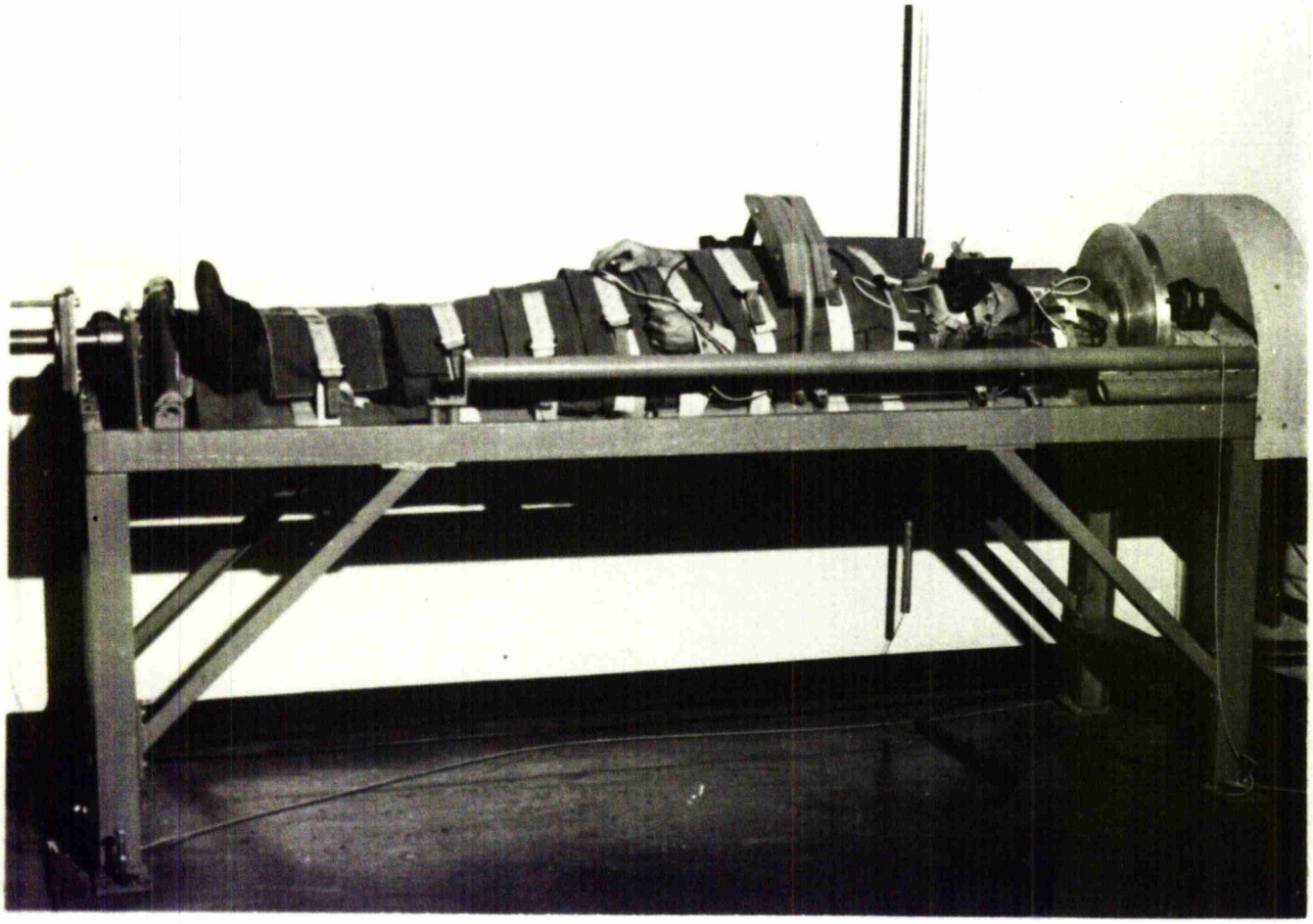


Figure 4.2

Rotating stretcher apparatus with subject strapped in position ready to commence the experiment.

METHOD

Apparatus

Rotation about a horizontal axis was carried out using a rigid metal stretcher, mounted in a substantial frame in which it was free to rotate continuously in either direction (Fig 4.2). Power was supplied by a small hydraulic motor (torque 25 lb.ft.), which could provide impulsive ($300^{\circ}/sec^{2}$) angular acceleration/deceleration stimuli. The speed of rotation could be controlled manually to an accuracy of $\pm 1^{\circ}$/sec over the range 5°/sec to 60°/sec. A tachogenerator and continuous sweep potentiometer were coupled to the stretcher, to provide angular velocity and position signals respectively. Pairs of small lights were placed above and below the stretcher at the level of the head, and used by the subject to make calibration eye-movements.

The subject was strapped to the stretcher in the supine position, with the axis of rotation coincident with the longitudinal axis of the body, by a firm canvas harness which extended from the shoulders to the ankles. Lateral body restraint was completed by adjustable rectangular metal plates which supported the shoulders on either side. Particular attention was paid to immobilisation of the head. The subject wore an R.A.F. aircrew helmet and face-mask

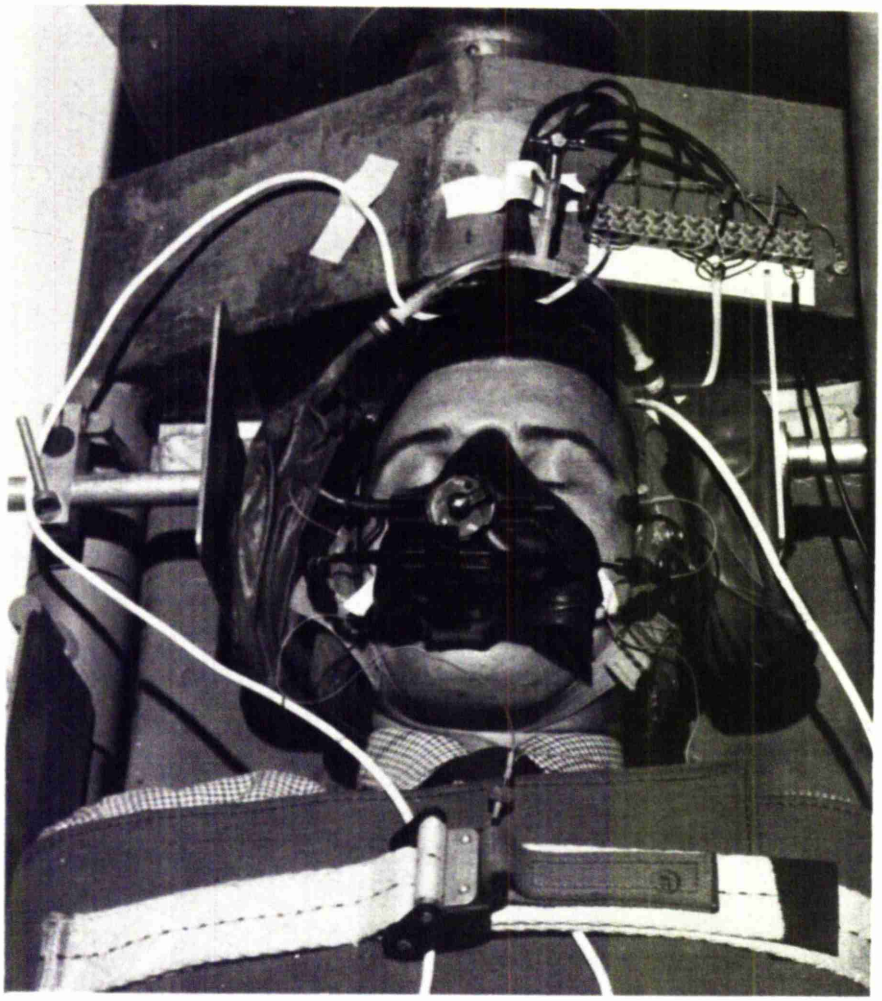


Figure 4.3

Close-up view of head end of the rotating stretcher to show method of head restraint and position of the electrodes.

assembly (Fig 4.3), firmly secured to the stretcher by adjustable straps, while polystyrene granule filled bladders were placed on either side of the head, and evacuated to form a rigid mould between the helmet and adjustable plates, which prevented lateral movement. The apparatus and special restraint methods used in this part of the experiment were designed by Dr. A. J. Benson. A more detailed description of this equipment is given in reference 20.

For rotation about a vertical axis, the turntable and chair assembly already described (Part 3 (2)) was used.

Horizontal eye-movements were recorded by DC electro-culography (Part 3 (3)) with the eyes closed and the face covered by a non-reflecting metal shield.

Conduct of Experiment

Ten laboratory personnel (7 male, 3 female) acted as subjects. After the nature of the experiment had been explained, the subject was strapped to the stretcher and the electrodes applied. Calibration eye-movements were recorded in the supine and the prone positions. The face shield was then clipped in position, and the subject instructed to relax with their eyes closed until the experiment was completed. Following impulsive acceleration to a pre-determined velocity, rotation continued for a minimum of

12 revolutions, though in some experiments up to 40 revolutions were made, before the stretcher was stopped with the subject in the supine position. Eye-movements were recorded continuously during rotation, and further calibration eye-movements were made between successive runs.

In a preliminary experiment using three subjects (Benson 1966, ref. 14) it was shown that there was no difference in the pattern of responses for rotation to the right and left. The main experiment was therefore carried out with rotation to the right only. Each subject experienced four runs, at different rotation velocities (60°, 40°, 20° and 10°/sec). The order in which these were presented was varied between subjects, but complete randomisation was not possible, as an appreciable number of subjects experienced nausea at the higher rotation rates, and it was usually advantageous to leave these until last.

A further experiment was also carried out on two subjects, in which the pattern of responses following impulsive acceleration was compared with that produced by acceleration at a near threshold rate. Each subject experienced initial accelerations of about 300°/sec^2 and 1°/sec^2, to a terminal velocity of 60°/sec to the right. Slow acceleration of the stretcher was obtained manually by opening the valve which controlled the oil flow to the hydraulic motor, in time with

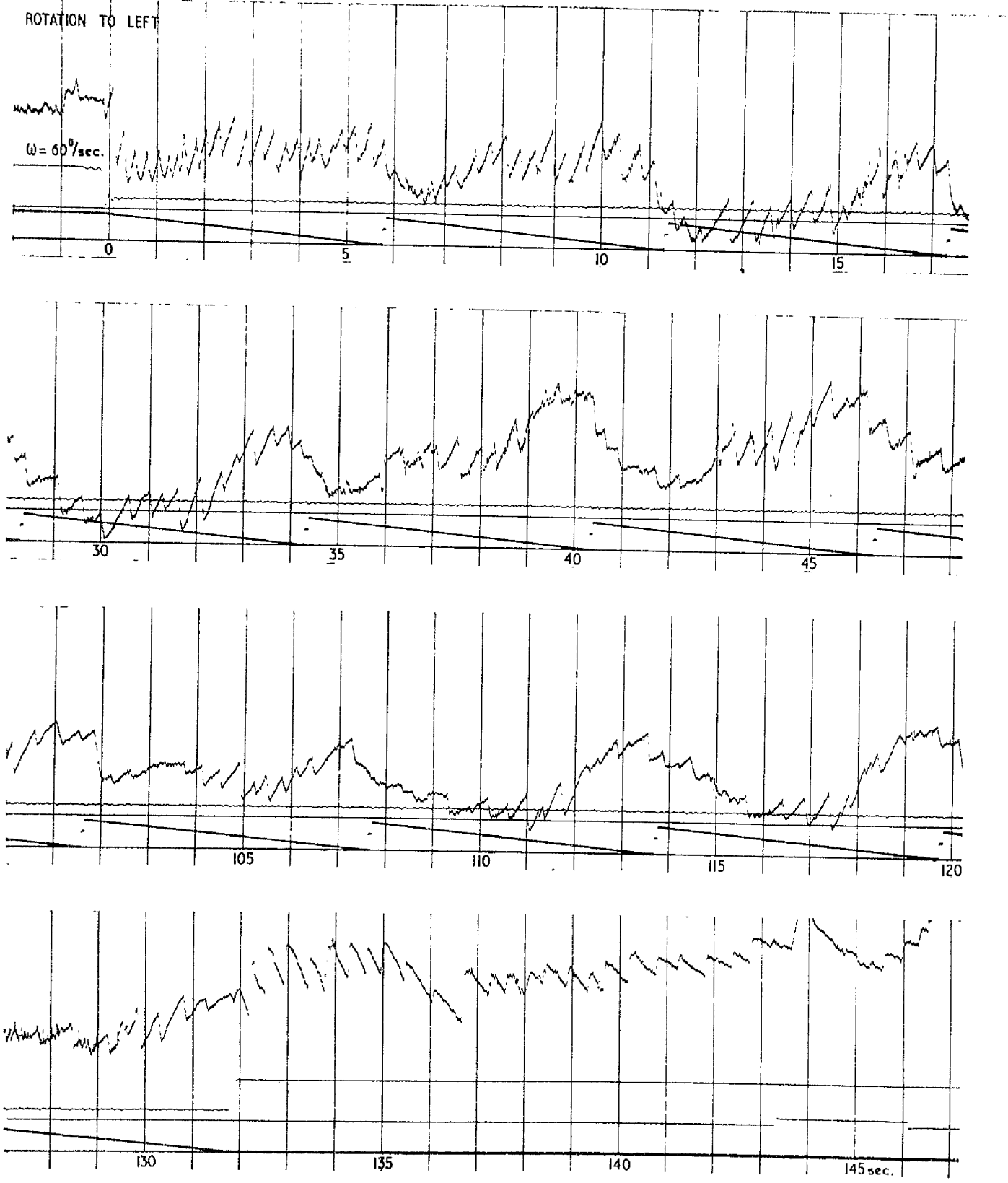


Figure 4.4

Record of lateral eye-movements obtained during and after rotation about a horizontal axis at 60°/sec. From above downwards the traces are: eye-movement, angular velocity of stretcher, subject's response and stretcher position. Vertical time markers are at 1 sec intervals. Rotation began at t = 0 sec and ended at t = 132 sec.

a stop watch. In all other respects the conduct of the experiment was as described.'

RESULTS

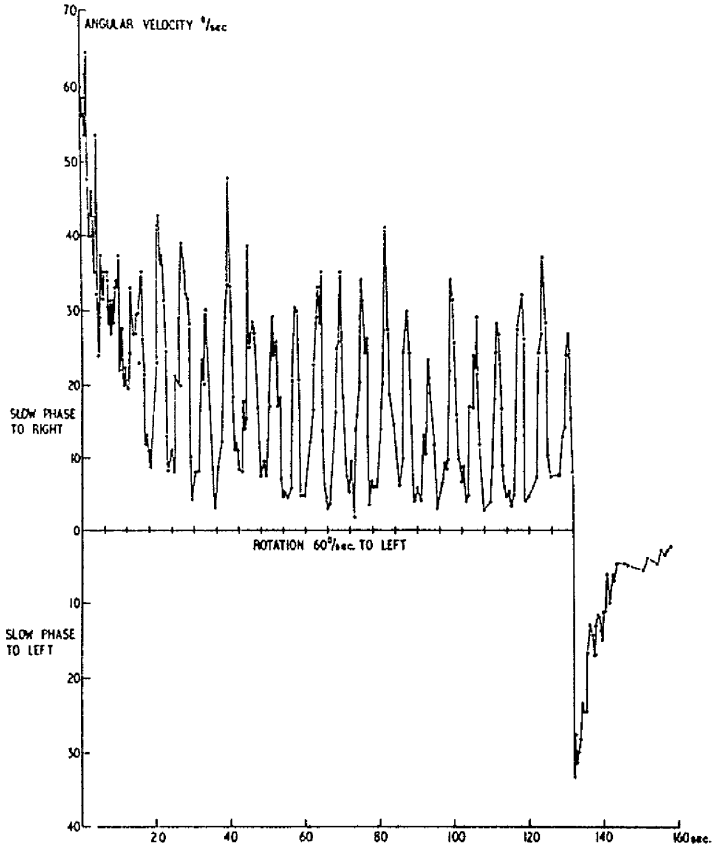
Subjective Experiences

Prolonged turning (3-4 min), especially at the higher rotation speeds, produced nausea in many of the subjects, and a number of potential subjects had to be excluded from the experiment on this account. Those who did not experience nausea, however, claimed to enjoy the sensations aroused by the rotation, particularly at the higher speeds.

All of the subjects also reported continuous sensations of turning throughout the period of rotation about the horizontal axis, in contrast to the rapid disappearance of turning sensations when the rotation axis was vertical (Part 3 (2)).

Per-rotational Eye-movements

Fig 4.4 shows a typical recording of lateral (horizontal) eye-movements obtained from one subject during rotation at 60°/sec to the right. At the commencement of rotation a sharp anti-compensatory eye-movement (Melvill Jones, 1964), i.e. in the same direction as the angular motion of the



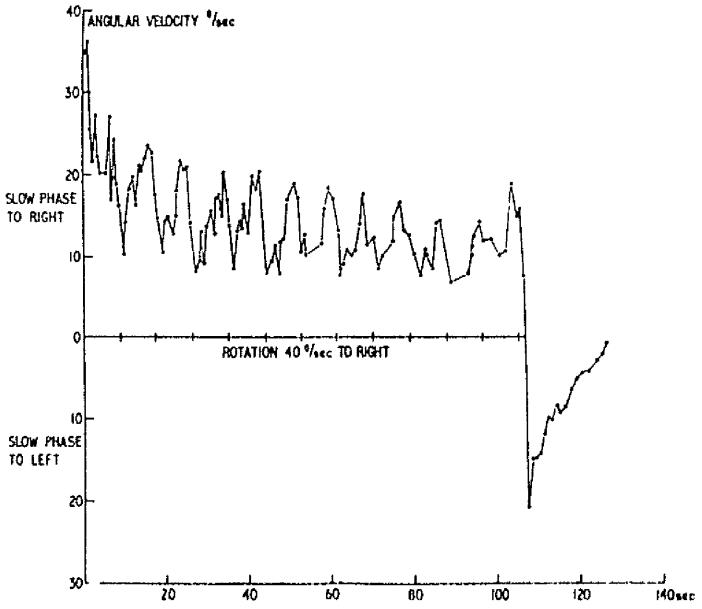


Figure 4.5a

Plot of slow phase nystagmus velocity against time, during and after rotation at 60° and 40° sec. Each division along the zero axis marks one cycle of rotation.

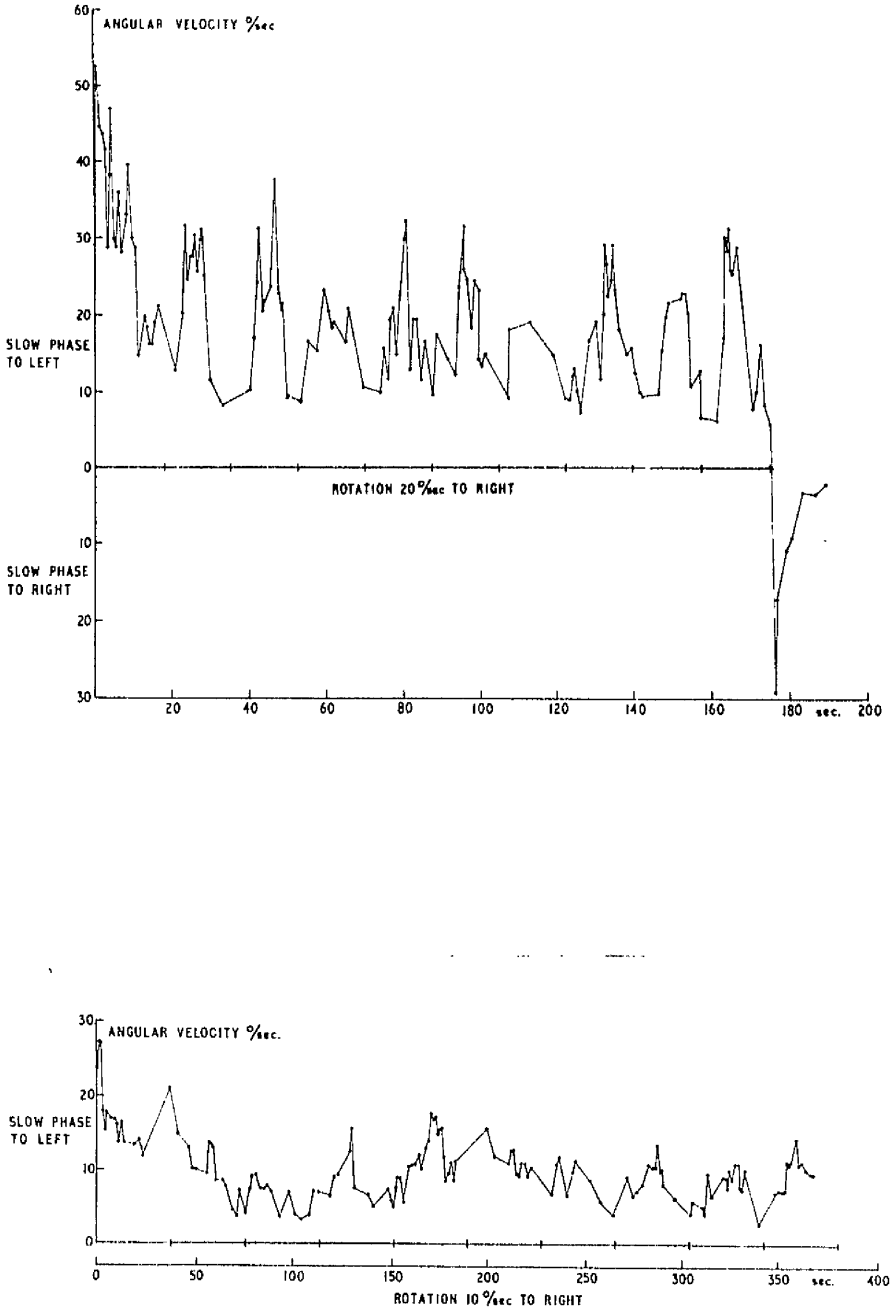


Figure 4.5b

Plot of slow phase nystagmus velocity against time, during and after rotation at 20° and 10°/sec. There was no post-rotational nystagmus in this subject following rotation at 10°/sec. Each division along the zero axis marks one cycle of rotation.

subject, was generally observed, and a similar though less marked deviation in the opposite direction when rotation ceased. These eye-movements were more apparent at the higher velocities of rotation. However, owing to the presence of a slow drift in potential during the period of recording, it was not possible to assess whether the mean deviation persisted throughout the period of rotation, or slowly returned towards the centre position during this time.

Compensatory nystagmus also developed, as soon as rotation commenced, i.e. with slow phase component which beat in the opposite direction to that of the angular motion, and was found to persist for as long as the rotation continued. This was in marked contrast to the exponential decay and disappearance of per-rotational nystagmus after about 30-40 sec when the subjects were rotated about the vertical axis (Part 3 (2)), although the plane of angular acceleration through the head was the same in each situation.

Quantitative evaluation of the eye-movement records was made as follows: the angular velocity of the slow phase component of each nystagmic beat, during the first twelve cycles of rotation, was calculated (Appendix 1A). These values were then plotted on a linear scale against time, and stretcher position, for each rotation speed. Fig 4.5 (a & b) shows the results for one subject. Following the initial acceleration to constant speed, the velocity of

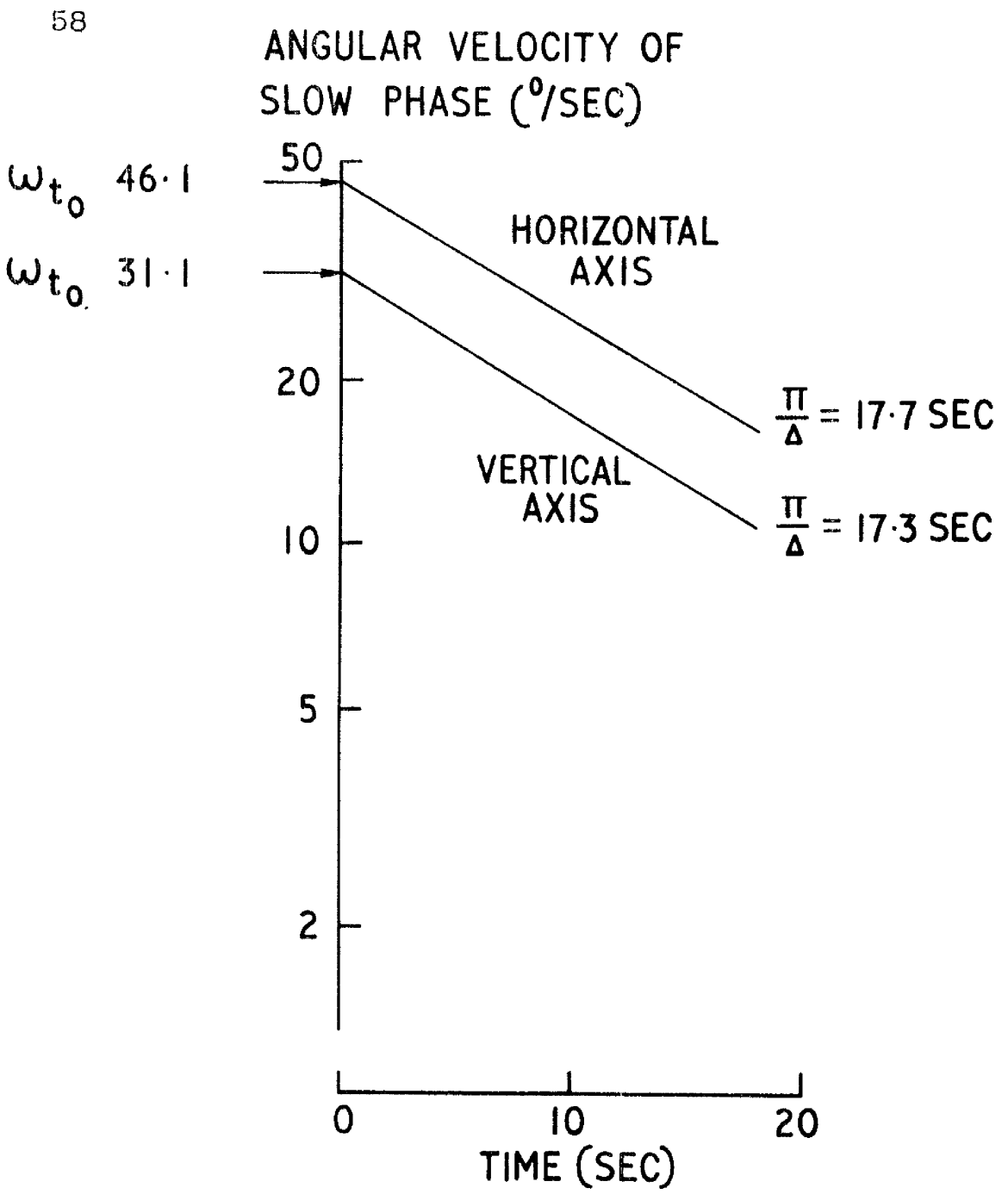


Figure 4.6

Comparison of mean pattern of decay of per-rotational nystagmus during the first three revolutions following impulsive acceleration in yaw to 60°/sec, about a vertical and a horizontal axis. Angular velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale. Based on results from 6 subjects. Initial slow phase velocity (ω_{to}) and time constant of decay (π/Δ) are indicated for each situation.

the slow phase component of per-rotational nystagmus decayed in an approximately exponential manner to about one third its initial value, over a period which occupied roughly the first 2-3 cycles of rotation. Thereafter a state of dynamic equilibrium ('steady-state' conditions) was established, in which the mean velocity of nystagmus remained approximately constant, though the velocity of sustained nystagmus was modulated in a cyclical manner which corresponded with the period of rotation of the stretcher.

The nystagmus slow phase velocity during the first three cycles of rotation was also plotted on a logarithmic ordinate scale against time (Fig 4.6), and the initial slow phase velocity and time constant of decay of nystagmus, for each subject, determined from the individual log-linear plots in the manner described in Appendix 1B. The mean time constant during this period (17.7 sec) did not differ significantly from that obtained when the same subjects were rotated about a vertical axis (17.3 sec). However, the initial slow phase velocity of per-rotational nystagmus was significantly higher ($p = 0.05$) for rotation about the horizontal axis (mean 46.1°/sec) than when the axis of rotation was vertical (mean 31.1°/sec) (Fig 4.6).

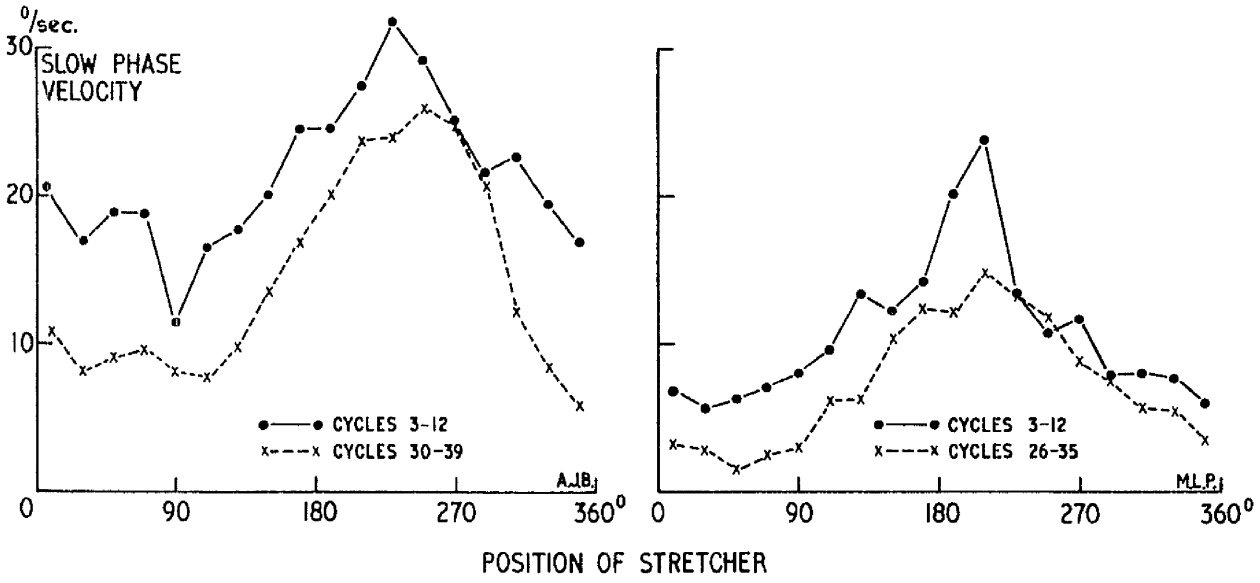


Figure 4.7

Comparison, in two subjects, of the mean pattern of nystagmus during ten cycles at the beginning and ten cycles at the end of prolonged rotation at 60°/sec. Each point is the mean velocity of slow phase nystagmus which occurred in each 20° arc.

To analyse the behaviour of the nystagmus with respect to time and position once 'steady-state' conditions had been reached, each of the ten cycles between the second and the thirteenth was divided into 20° intervals. These intervals contained comparable numbers of nystagmus beats at the different rotation rates. The mean velocity of the slow phase of all nystagmic beats in each interval was calculated, and corresponding values over the ten cycles averaged together, to give 18 nystagmus velocity values for each rotation speed. From these the average pattern of nystagmus slow phase velocity during one cycle of rotation (i.e. an angular displacement of the subject of 360°) was obtained.

The records from two of the subjects contained inadequate nystagmic eye-movements, but in the remaining eight subjects, sustained nystagmus was recorded at all rotation speeds. There were minor changes in amplitude and frequency of these eye-movements, but otherwise the nystagmus was found to persist without significant alteration for as long as rotation continued - namely 5 min. at 60°/sec and 6 min. at 10°/sec. During prolonged rotation, a slight reduction in the mean slow phase velocity was observed, as is shown in Fig 4.7 for two subjects who experienced extended rotation at 60°/sec, but there was no alteration in the form of the cyclical modulation of nystagmus velocity.

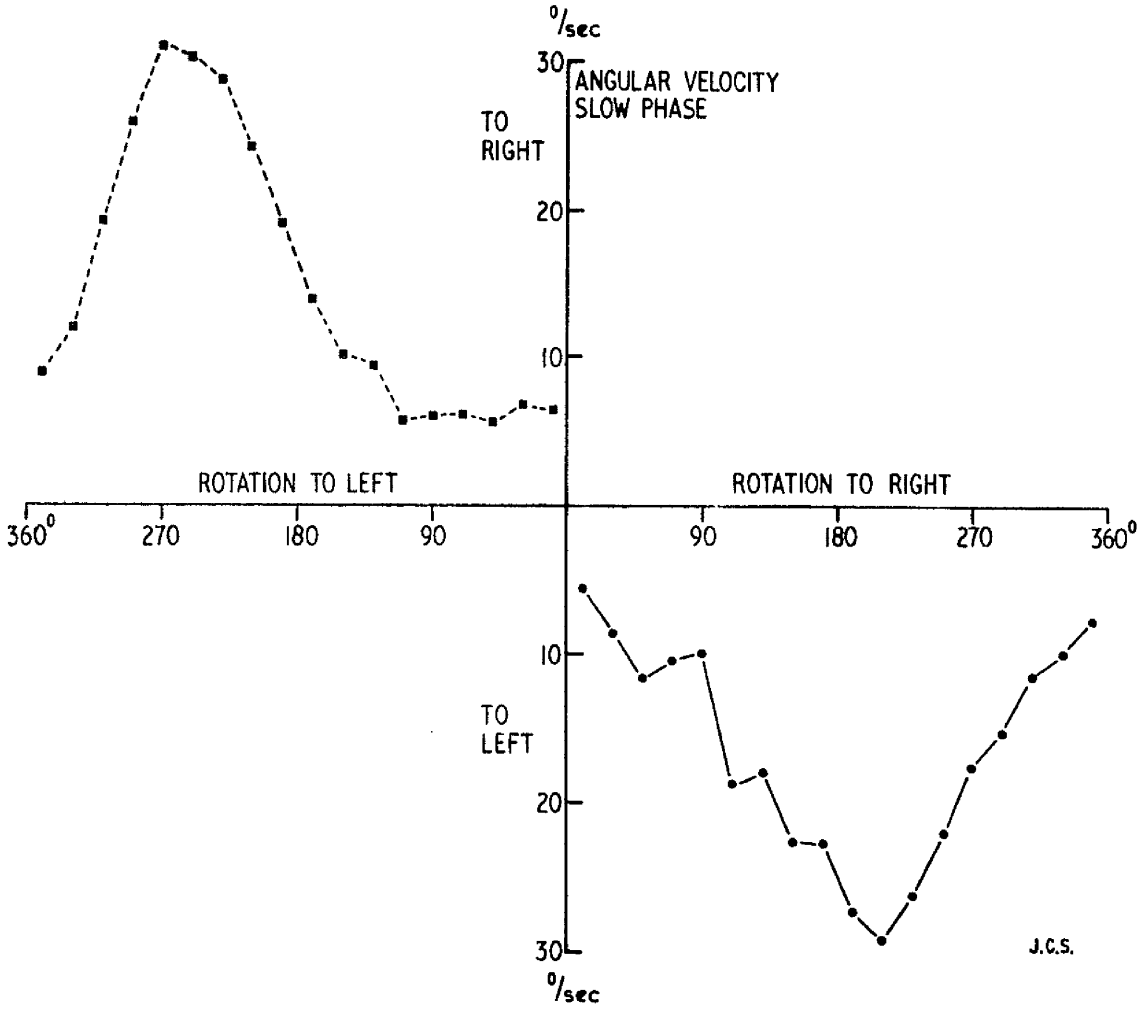


Figure 4.8

Plot of slow phase velocity of per-rotational nystagmus against stretcher position in one subject, for rotation to the left and the right at 60°/sec. Each point is the average value, over ten cycles, of the velocity of nystagmus which occurred in each 20° arc.

In the preliminary experiments in which subjects were rotated both to the right and the left (Benson 1966, ref.13) the slow phase component of the per-rotational nystagmus was always in the opposite direction to the motion of the stretcher. In addition, the modulation of nystagmus was found to be of a similar pattern irrespective of the direction of rotation (Fig 4.3). Accordingly, in the main experiment, the more detailed study of the effect of speed of rotation on the nystagmic response was made for rotation in one direction only.

Per-rotational nystagmus was characteristically superimposed on slow cyclical swings in potential (Fig 4.4), a feature which was present at all speeds, though it was less apparent at the slower rotation rates. In seven subjects these were of a sinusoidal form, which corresponded with the period of rotation of the stretcher, but in the other three subjects no consistent cyclical waveform was apparent. It was not possible to establish unequivocally the true cause of these potential swings, but irrespective of whether they were artefacts, a manifestation of eye-movements, or a combination of both, they introduced errors into the measurements of angular velocity of the slow phase nystagmus components. For example, if the trace drifted in a direction equivalent to an eye-movement to the right, the apparent

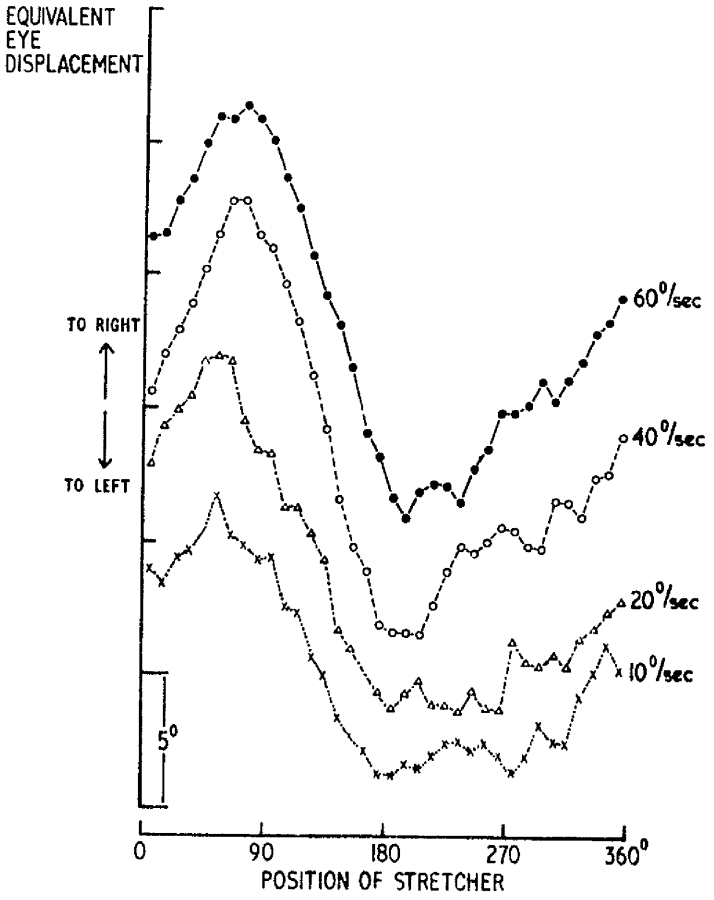


Figure 4.9

Comparison for each rotation speed of the pattern of potential swings, on which nystagmus was superimposed, plotted as equivalent eye displacement. Each curve is the average for ten cycles in seven subjects.

velocity of nystagmus with a slow phase component in that direction would be increased, and conversely the velocity of nystagmus to the left decreased. Accordingly, to obtain the true velocity of eye-movement, it was necessary to correct the measures of nystagmus slow phase velocity, by addition or subtraction of the equivalent angular velocity component of the slow potential swing on which the nystagmus was superimposed.

The corrections to be applied were determined in the following manner. Each cycle on the record was divided into 10^0 intervals, and the mean ordinate value in each interval measured with a Benson-Lehner OSCAR trace-measuring instrument. Corresponding values were then averaged over the ten cycles, and plotted to give mean displacement curves for each speed of rotation. Fig 4.9 illustrates the time course of the slow potential swings in the seven subjects in whom a common pattern emerged. The OSCAR data was also analysed by digital computer, and the most appropriate polynomial equation for each displacement curve determined empirically, and differentiated to obtain the corresponding equation which described equivalent eye angular velocity during each revolution. These equations were then solved for the 18 positions at which the mean nystagmus velocity had been determined, and the appropriate corrections applied in order to obtain the true nystagmus slow

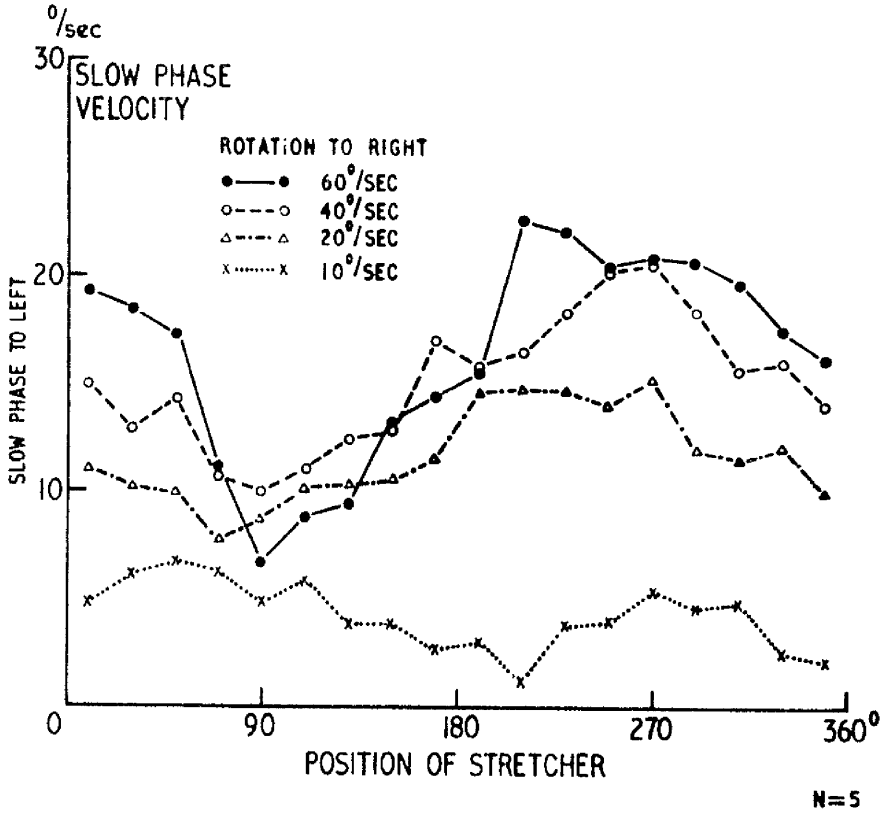


Figure 4.10

Plot of slow phase velocity of per-rotational nystagmus against stretcher position at four speeds of rotation. Each point is the mean, in five subjects, of the velocity of nystagmus which occurred during each 20° arc. At 0° and 360° the subjects were supine and at 180° prone.

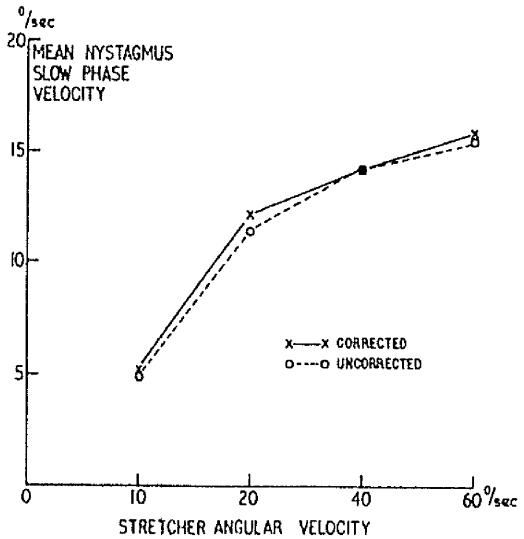


Figure 4.11

Comparison of the mean velocity of slow phase nystagmus at each rotation speed, before and after correction for the effects of the potential swings on which nystagmus was superimposed. Each point is the mean value over ten cycles in eight subjects.

phase velocity at these points.

Correction of the slow phase velocity in this manner changed the form of the plot of nystagmus velocity against stretcher position, from the simple curve exemplified by Figs 4.7 and 4.8 to one of a more sinusoidal form (Fig 4.10). Greater changes occurred at the higher rotation speeds, where the angular velocity of the slow potential swings was proportionately greater. However, as these swings were approximately symmetrical, there was little alteration in the mean velocity at each speed of rotation. This is shown in Fig 4.11, which is a plot of the average for eight subjects of the mean slow phase velocity of uncorrected and corrected nystagmus at each rotation speed.

When the graphs of corrected nystagmus velocity against stretcher position were compared, two main cyclical patterns emerged. The commonest was roughly sinusoidal in form, with a single maximum velocity peak in the arc 200°-300°, illustrated in Fig 4.10 which is the mean of five subjects who produced this pattern of response. In a second group of three subjects, peak nystagmus velocity occurred twice during each cycle, and the mean curve for these subjects is shown in Fig 4.12. These two groups were not dissimilar, however, differing only by a degree of phase compression, and they have been combined together in Fig 4.13 to give a more

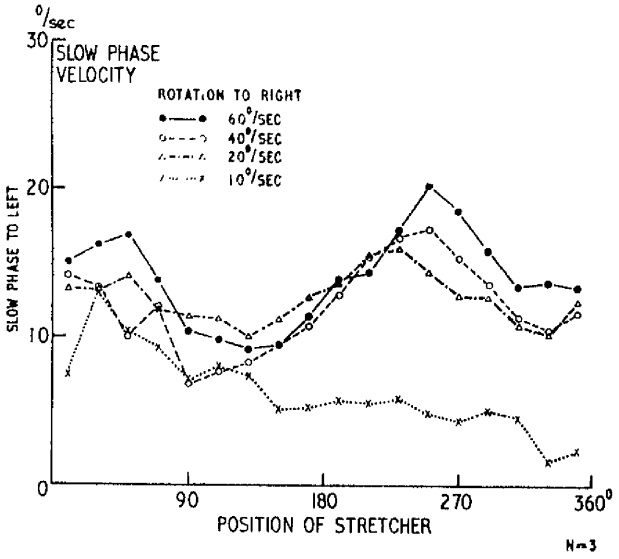


Figure 4.12

Plot of slow phase velocity of per-rotational nystagmus for three subjects, as in Figure 4.10.

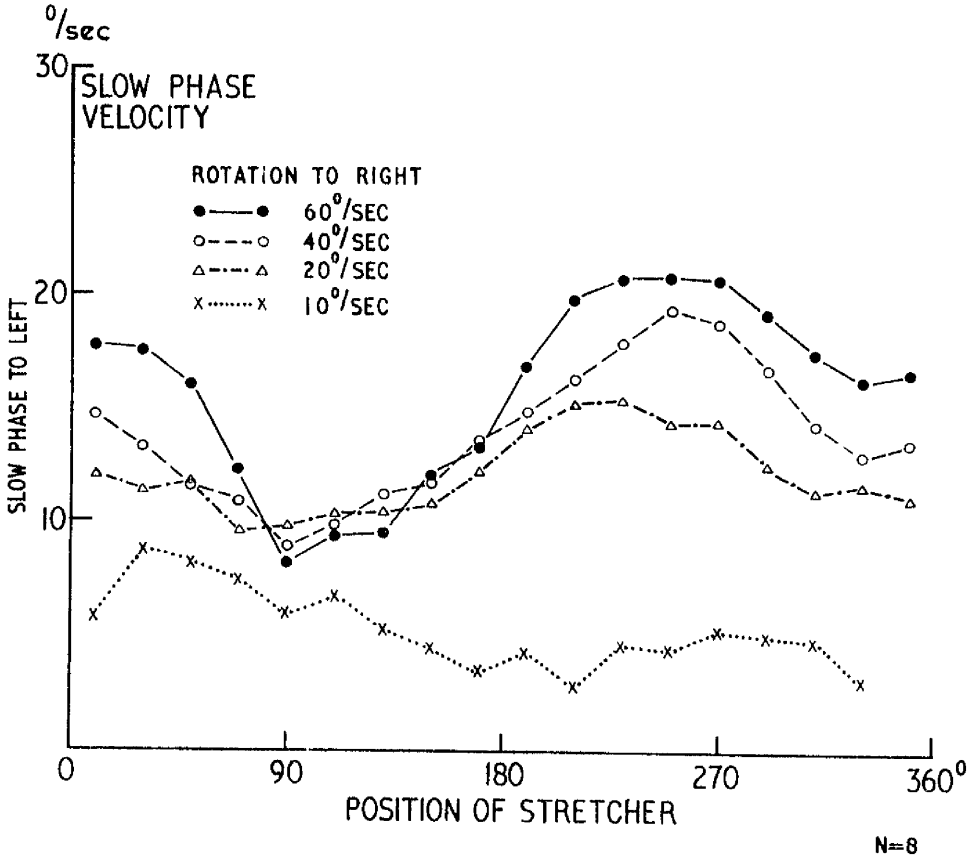


Figure 4.13

Plot of slow phase velocity of per-rotational nystagmus for the eight subjects depicted in Figures 4.10 and 4.12.

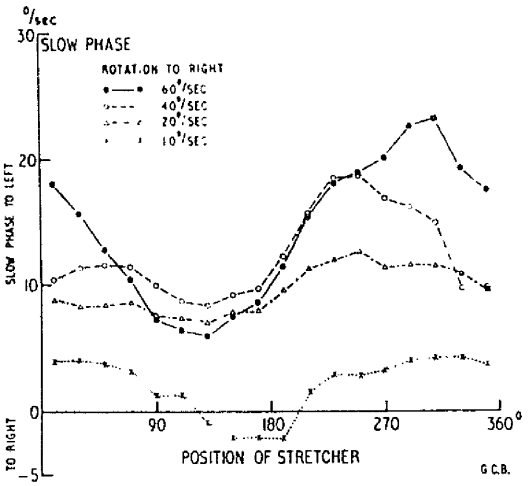


Figure 4.14

Plot of slow phase velocity of per-rotational nystagmus, as in Fig 4.10, for one of the two subjects who showed reversal of nystagmus over the arc 120°-200° during rotation at 10°/sec.

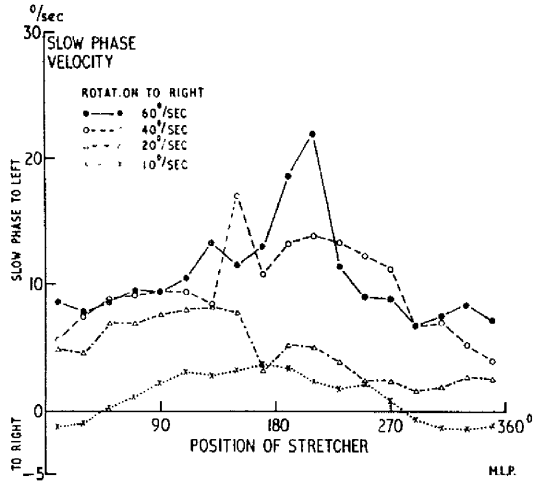


Figure 4.15

Plot of slow plase velocity of per-rotational nystagmus for one subject, as in Fig 4.10. This subject showed reversal of nystagmus during rotation at 10°/sec over the arc 300°-040°.

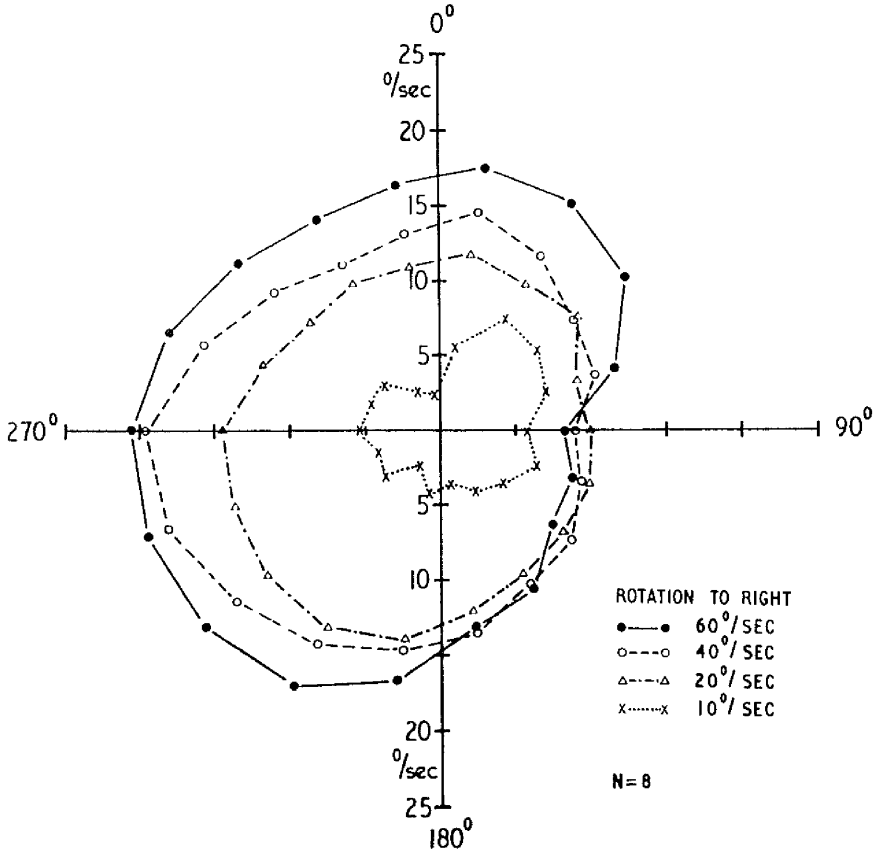


Figure 4.16

Plot in polar co-ordinates of slow phase velocity of nystagmus against stretcher position for the eight subjects depicted in Fig 4.15.

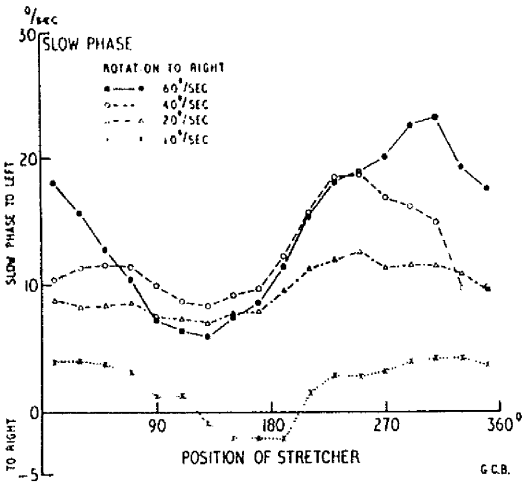


Figure 4.14

Plot of slow phase velocity of per-rotational nystagmus, as in Fig 4.10, for one of the two subjects who showed reversal of nystagmus over the arc 120°-200° during rotation at 10°/sec.

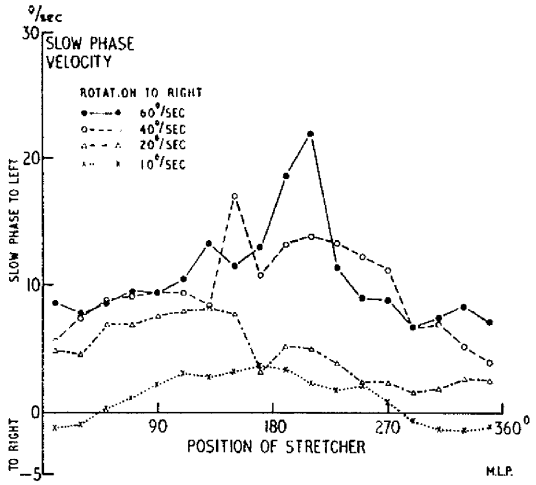


Figure 4.15

Plot of slow plase velocity of per-rotational nystagmus for one subject, as in Fig 4.10. This subject showed reversal of nystagmus during rotation at 10°/sec over the arc 300°-040°.

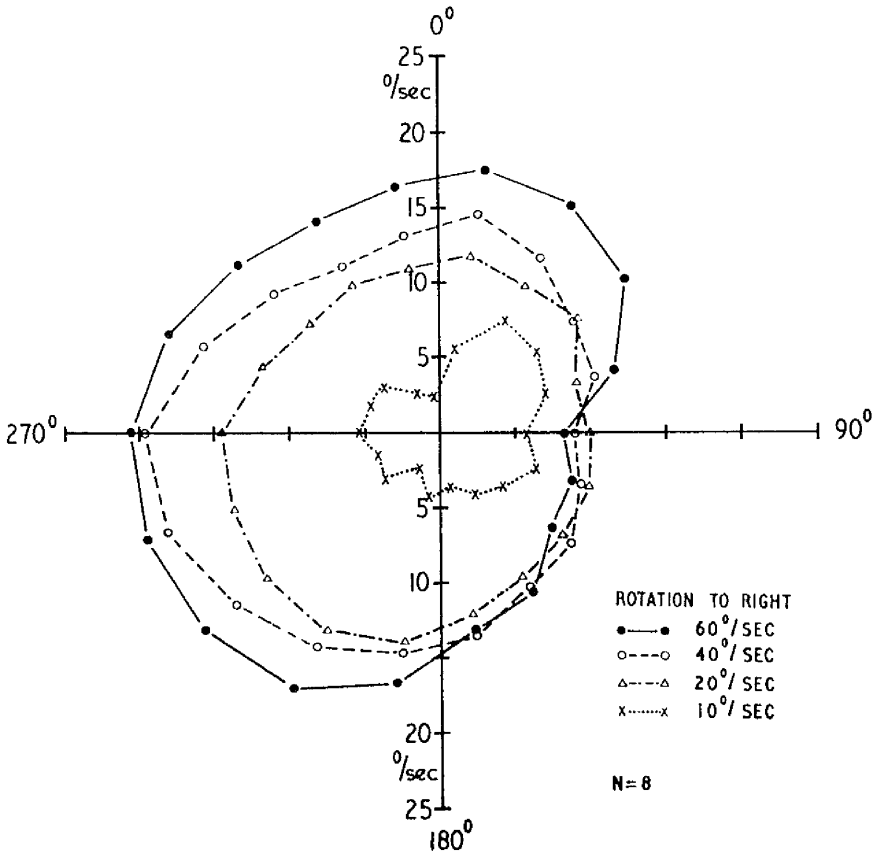


Figure 4.16

Plot in polar co-ordinates of slow phase velocity of nystagmus against stretcher position for the eight subjects depicted in Fig 4.15.

representative picture.

In the experiments of earlier workers, in which the direction of the linear acceleration vector was stable, or changed only slowly, the direction of nystagmus was shown to be dependent on that of the linear acceleration (Aschan et al, 1957; Benson, 1962; Lansberg, Guedry and Grabiel, 1964). Accordingly in the present experiment regular reversal of nystagmus might have been expected to occur, but it was observed only in four subjects and only at the slowest speed of rotation (10°/sec). In one subject reversal was present for the whole of the second half of the cycle (150°-360°), in two subjects only over the arc 120°-200° (Fig 4.14), and in the fourth subject when they were passing through the supine position (300°-040°) (Fig 4.15).

At speeds greater than 10°/sec there was no change in the direction of nystagmus, which continued to beat with a slow component opposite to the angular motion of the stretcher for as long as rotation continued. The velocity of the sustained nystagmus increased progressively with the speed of rotation of the stretcher, except in the quadrant 90°-180°, where it appeared (at all but the slowest speed) to be independent of stretcher velocity. This is illustrated more clearly when the data in Fig 4.13 is plotted in polar co-ordinates (Fig 4.16).

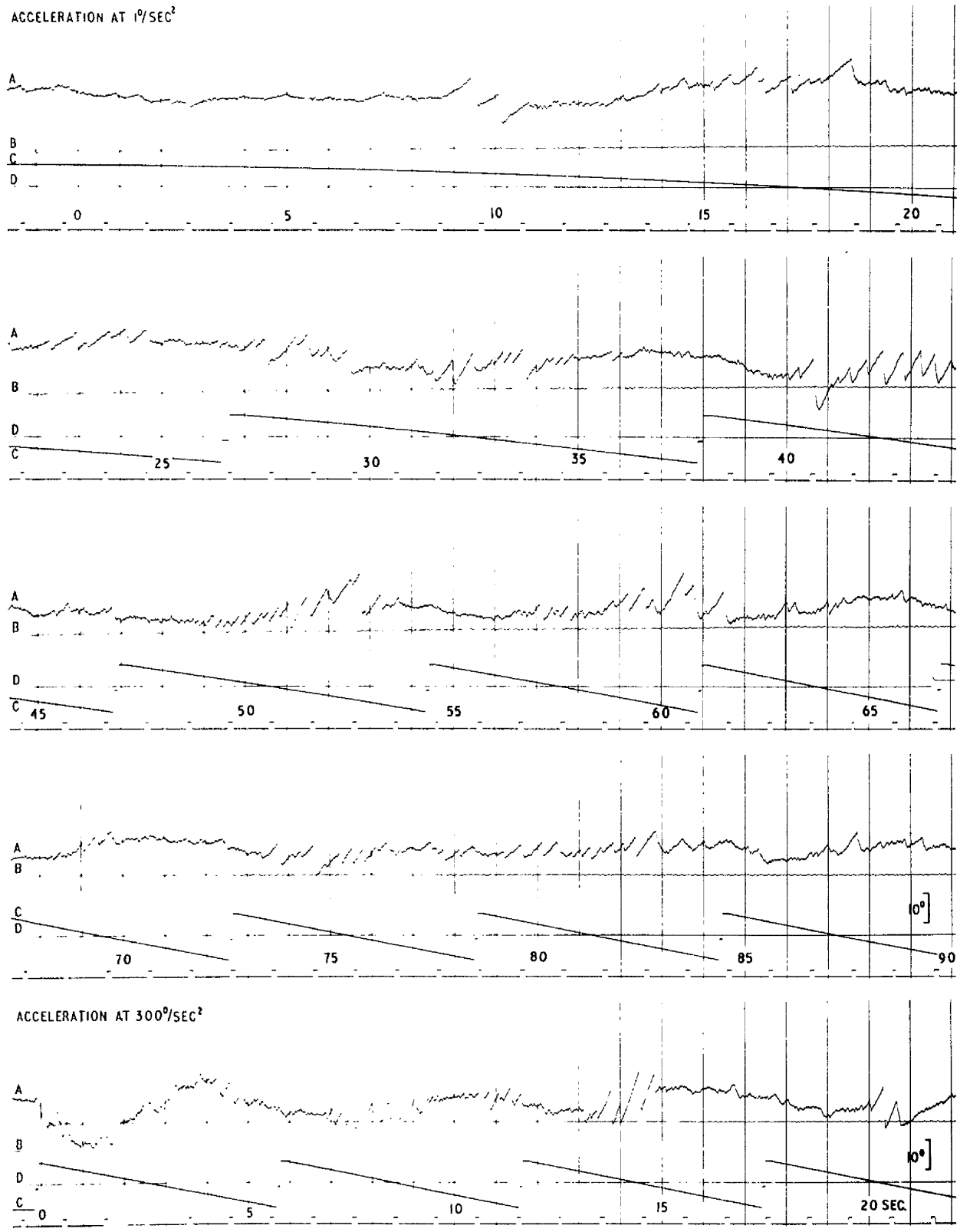


Figure 4.17

Records of horizontal eye-movements recorded from one subject during acceleration at $1°/sec^2$ and $300°/sec^2$ to a velocity of 60°/sec to the right. Each record also shows the first four cycles of rotation after acceleration had ceased. The traces are: A eye-movement, B angular velocity of stretcher, C stretcher position, and D marker to indicate beginning and end of acceleration. Vertical time markers are a 1 sec intervals. On the top record acceleration at $1°/sec^2$ commenced at t=0 sec and ended at t=66.5 sec.

Comparison of Per-rotational Nystagmus following Impulsive and Slow Accelerations

The sustained nystagmic response observed in the main experiment might have been influenced by the stimulus to the canal receptors provided by the relatively high initial angular acceleration. Accordingly a further experiment was carried out on two subjects, to compare the pattern of nystagmus during 'steady-state' conditions following the impulsive ($300^{\circ}/sec^{2}$) acceleration routinely used in this study, with that obtained after accelerations at a near threshold rate ($1^{\circ}/sec^{2}$).

Fig 4.17 shows the eye-movement records from one subject during the phase of slow acceleration and the ensuing four cycles of constant velocity rotation. The first four cycles following impulsive acceleration in the same subject are also shown for comparison. At the commencement of the slow acceleration there was slight angular 'cogging' of the stretcher, until a velocity of $2^{\circ}/sec$ was reached, but this did not affect the pattern of eye-movements. Thereafter a fairly uniform acceleration of just under $1^{\circ}/sec^{2}$ was achieved in both subjects.

Nystagmus, with slow phase component to the left, appeared after about 9 secs, and thereafter developed progressively, both in amplitude and slow phase velocity, as the acceleration continued. Cyclical modulation of the pattern

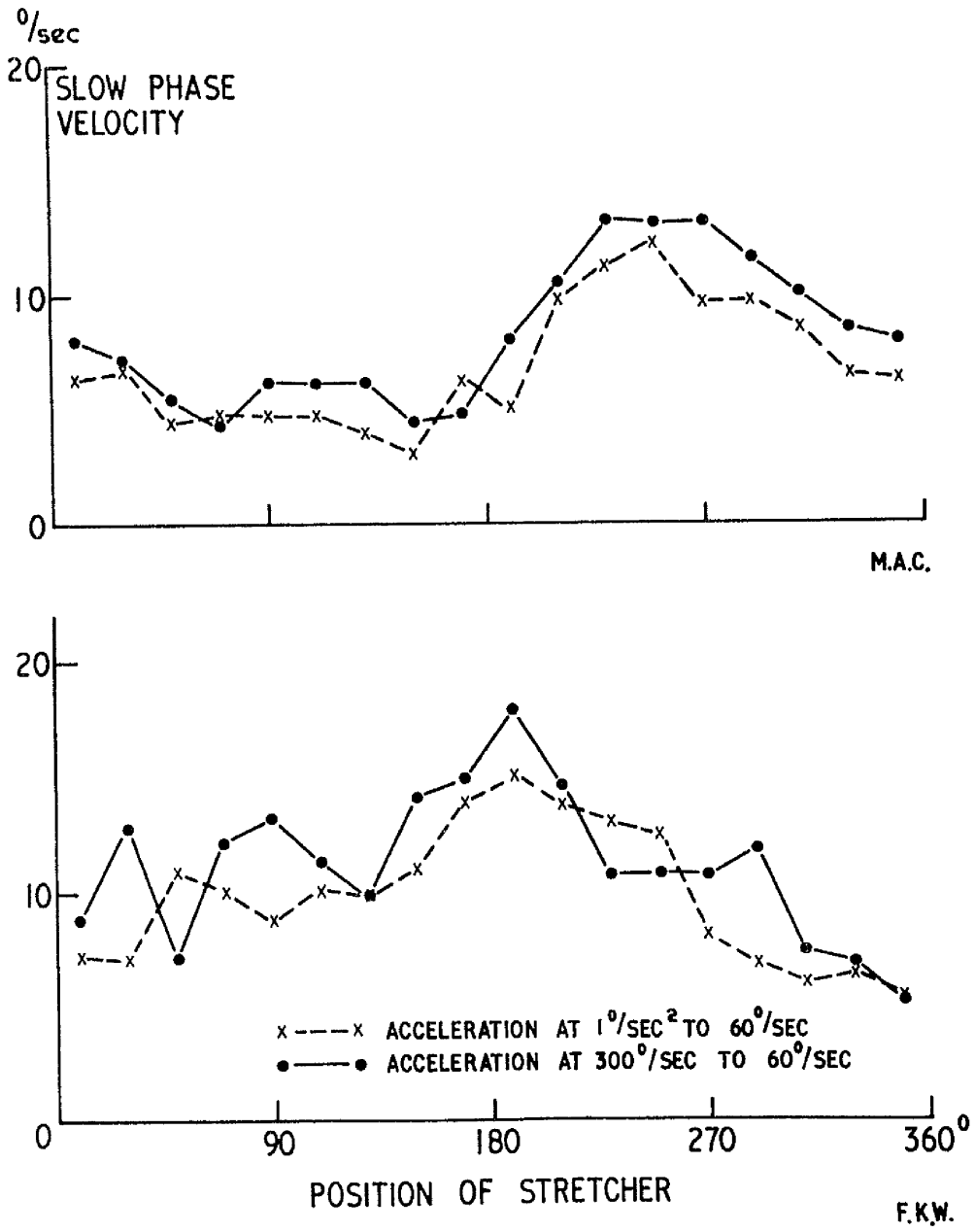


Figure 4.18

Plots of slow phase velocity of per-rotational nystagmus against stretcher position for two subjects, following slow and rapid accelerations. Each point is the average over 10 cycles (Nos 4 to 14) of the velocity of nystagmus which occurred in each 20° arc.

of nystagmus was apparent from the second cycle of rotation onwards, and in the latter stages of acceleration showed a well established positional dependence, which was maintained throughout the ensuing period of rotation at constant velocity.

The eye-movement records for ten cycles from the third to the fourteenth in each run were analysed quantitatively in the manner already described, and the mean curves obtained in each subject were found to be independent of the pattern of the initial acceleration (Fig 4.18).

SUMMARY

A revolving 1'g' linear acceleration vector in the transverse plane of the skull, produced by rotation about a horizontal cephalo-caudal axis, was found to produce sustained compensatory lateral nystagmus for as long as rotation continued. The velocity of slow phase nystagmus showed a cyclical modulation, the amplitude of which increased with the speed of rotation. This was in marked contrast to the exponential decay and disappearance of per-rotational nystagmus, within 30-40 sec, when a similar angular stimulus was applied with the axis of rotation vertical.

The findings indicate that following stimulation of the lateral semicircular canals, the pattern of responses to angular motion was altered when the gravitational acceleration

lay in the transverse plane of the head (compared with those obtained when the gravity vector was normal to that plane) in a manner related to the velocity of rotation of the gravitational vector, but independent of the magnitude of the initial angular acceleration.

The results will be discussed in detail in Part 6.

PART 4.

Section 2

Comparison of Vestibular Responses During Rotation in Pitch about Vertical and Horizontal Axes

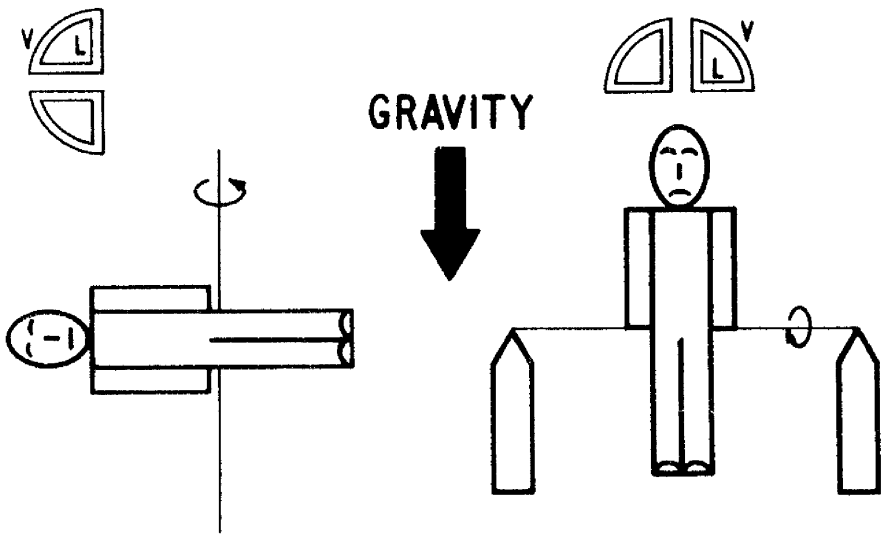


Figure 4.19

Diagram to illustrate the experimental situations for rotation in pitch (sagittal body plane) about a vertical (left) and horizontal axis (right). The orientation of the vertical semicircular canals (V) to the plane of rotation was the same in each situation. During rotation about the horizontal axis there was continuous reorientation of the body relative to gravity, as well as rotation of the g-vector in the sagittal plane of the skull. These features were not present when the axis of rotation was vertical.

SECTION 2

COMPARISON OF VESTIBULAR RESPONSES DURING ROTATION IN PITCH ABOUT VERTICAL AND HORIZONTAL AXES

Purpose of Experiment

The findings in the previous section were concerned only with responses from the horizontal semicircular canals. Irrespective of the underlying mechanism, however, it seemed likely that comparable differences would also be present in the pattern of responses following stimulation of the vertical canals, in the presence and the absence of a rotating component of g-vector in the sagittal plane of the skull. Accordingly the present experiment, essentially similar in principle to the previous one, was carried out to compare the pattern of responses during continuous rotation in pitch about a horizontal axis, with those obtained when the axis of rotation was vertical (Fig 4.19).

In both situations the orientation of the vertical semicircular canals to the plane of rotation was the same, so that the ampullary receptors of these canals experienced a similar stimulus from the angular acceleration in each situation.

During rotation about the horizontal axis, as well as rotation of the g-vector in the sagittal plane of the head, there was also continuous reorientation of the subject relative to gravity, as in the previous experiment. Rotation about the vertical axis, however, did not produce a change in orientation of the subject to the gravitational vector, so that neither feature was present in these circumstances.

As well as rotation in pitch about two orthogonal axes, rotation in yaw about a vertical axis was also carried out at part of the experiment, so that differences between the pattern of responses from the lateral and vertical canals could be compared in the same group of subjects.

When the rotation axis was horizontal, preliminary experiments revealed that the pattern of responses in pitch was not symmetrical, as in the previous experiment, but differed according to the direction of turning. The main part of this experiment was therefore carried out with rotation both in the forward and backward directions. Only a single velocity of rotation, however, (60°/sec) was used in the experiment. This was due to limitations in the structural stability of the apparatus for horizontal axis rotation at higher speeds, while slower rotation velocities were usually insufficient to evoke an adequate nystagmic response from the vertical canals.

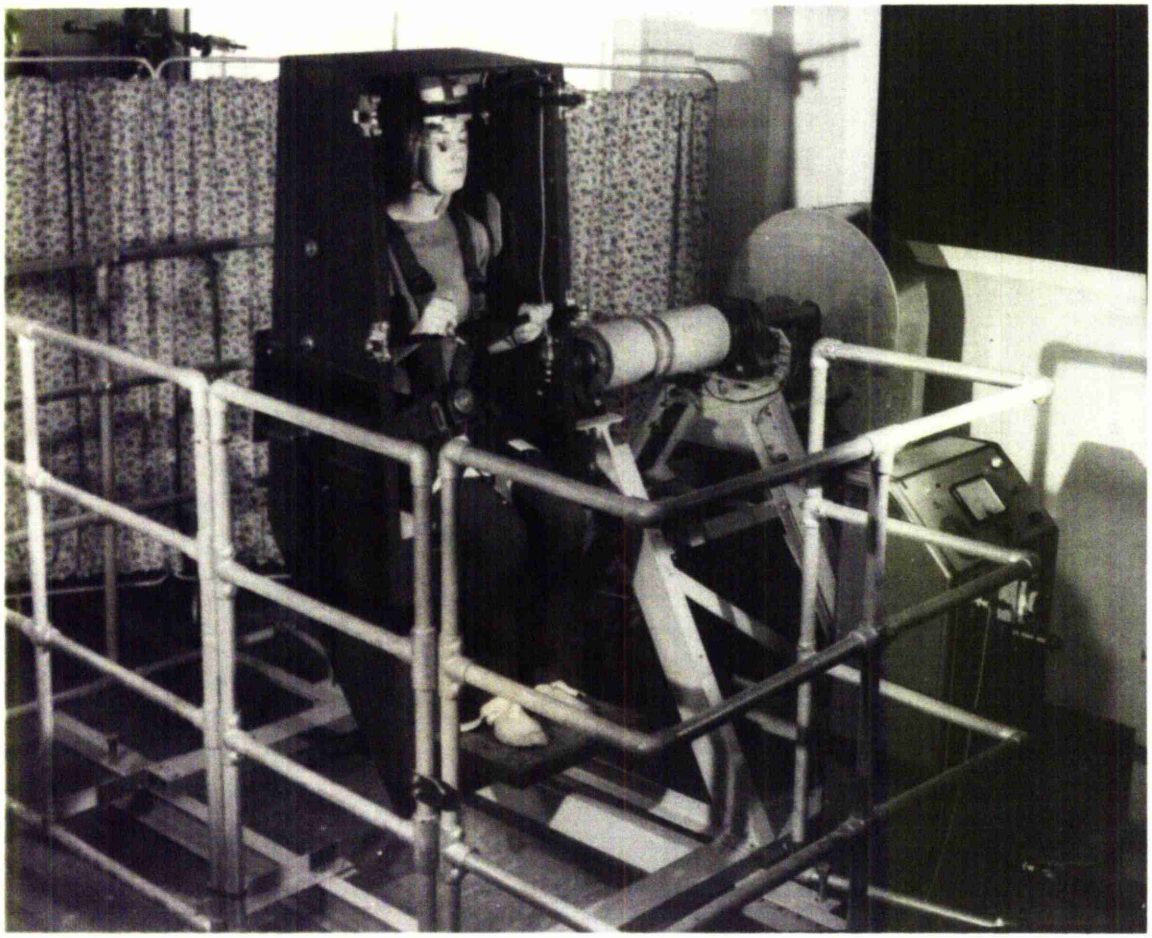


Figure 4.20

Apparatus for rotation in pitch about a horizontal axis, with subject strapped in position ready to commence an experiment. Controls for the hydraulic power system are mounted at rear right of the guard-rail.

METHOD

Apparatus

Rotation about a horizontal axis was carried out with the subject seated in a partially enclosed rectangular wooden chair, mounted on the end of a horizontal axle which coincided closely with the centre of gravity of the average subject. The chair was free to rotate continuously in either the forward or backward direction (Fig 4.20). Power was supplied by the same hydraulic motor and control system used in the previous 'rotating stretcher' experiment. A tachogenerator was coupled to the axle, and a microswitch actuated when the chair was vertical, to provide angular velocity and position signals respectively. A pair of small lights was placed vertically in front of the chair at the level of the head, and used by the subject to make calibration vertical eye-movements.

The subject was secured in position with the chair upright by a standard aircrew harness, while further restraint was provided by an additional strap between the legs to 'anchor' the lap belt to the seat, as well as thigh and foot straps. Adjustable metal side plates supported the shoulders, and a bar was placed across the front of the chair for the subject to grip. The head was immobilised by an adjustable

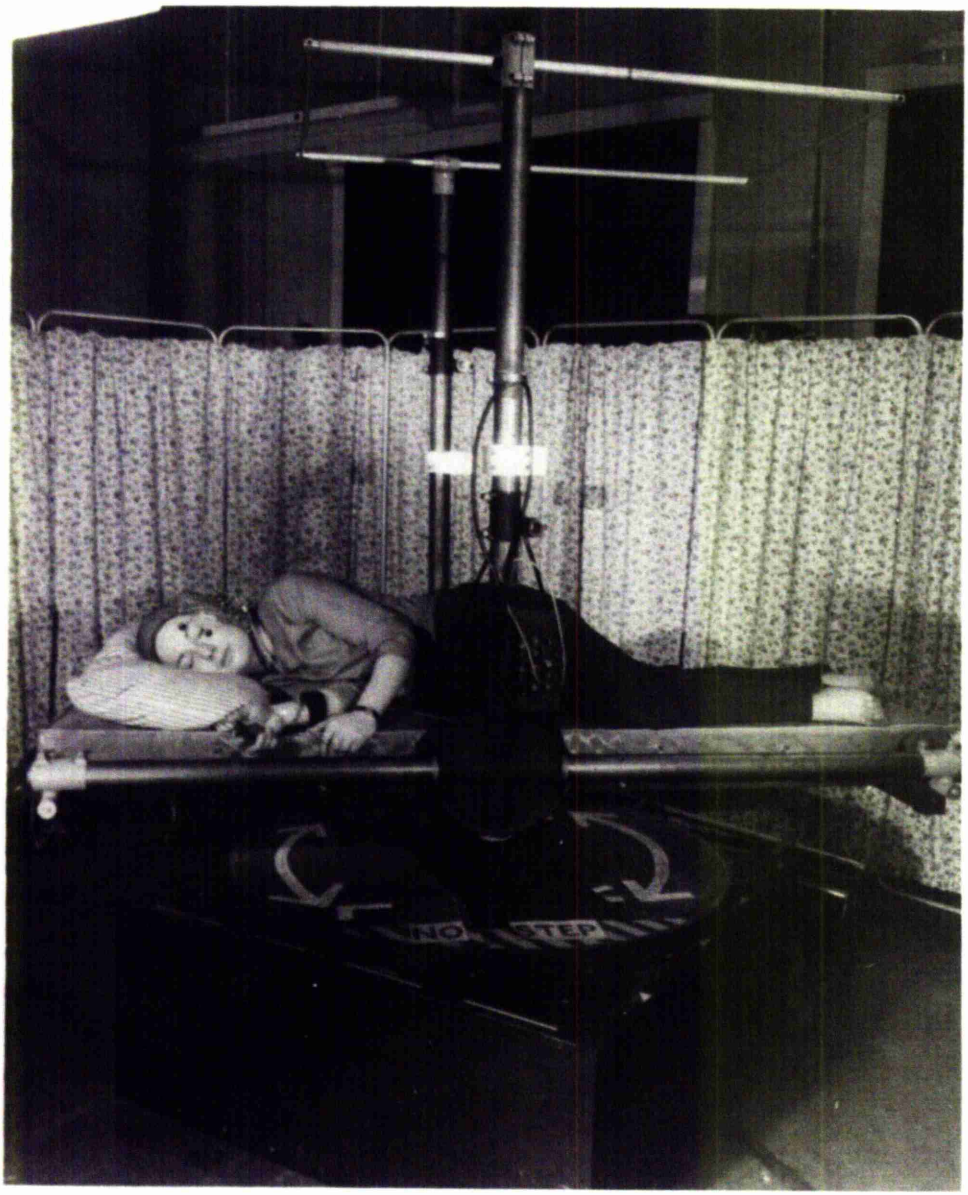


Figure 4.21

Turntable assembly with subject in position for rotation in pitch about a vertical axis. Note placement of the electrodes for recording vertical eye-movements from the left eye.

padded forehead clamp (Fig 4.20).

For rotation about a vertical axis in pitch and yaw, the turntable already described (Part 3 (2)) was used, with the subject seated upright for stimuli in yaw (Fig 3.2), or lying horizontally on their right side for stimuli in pitch (Fig 4.21). As in the main experiment, rotation in both these procedures commenced with a rapid acceleration to 60°/sec, and continued for 10 revolutions, both in the clockwise and counterclockwise direction.

During rotation in pitch, vertical eye-movements were recorded from the left eye by DC electroculography (Part 3 (~~5~~ 3)), with the eyes closed.

Conduct of Experiment

Ten laboratory personnel (4 male, 6 female) acted as subjects.

After the nature of the experiment had been explained, the elctrodes were applied, the subject strapped into the chair, and a signalling key placed in their hand. Calibration eye-movements were recorded with the chair upright, and the subject was then instructed to relax with their eyes closed until the experiment was completed. As in the previous experiment, rotation commenced with an impulsive acceleration ($300^{\circ}/sec^2$) to 60°/sec, and continued for 12 revolutions (72 sec), before the chair was stopped by an impulsive

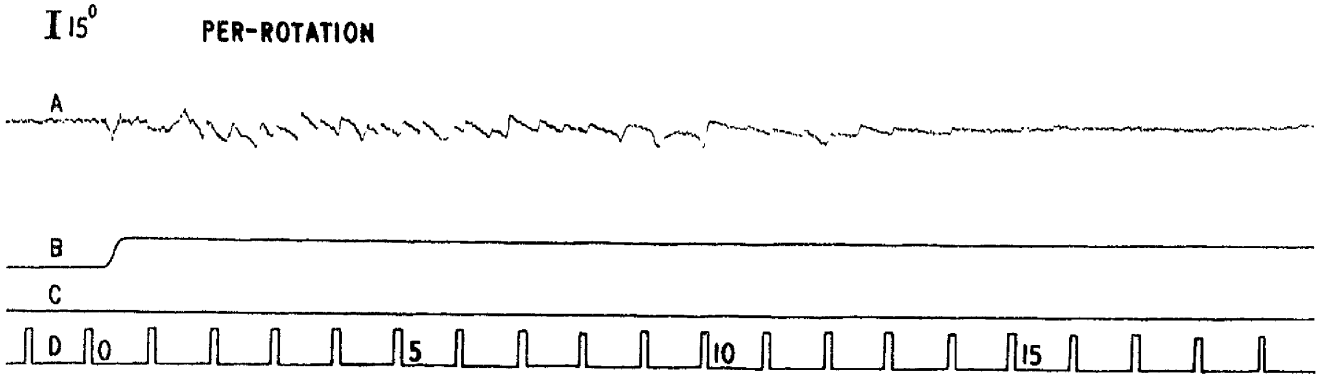


Figure 4.22

Record of vertical eye-movements obtained from one subject during forward rotation in pitch at 60°/sec about a vertical axis. The traces are: A eye-movements, B tachogenerator signal, C not in use, D 1 sec time marker.

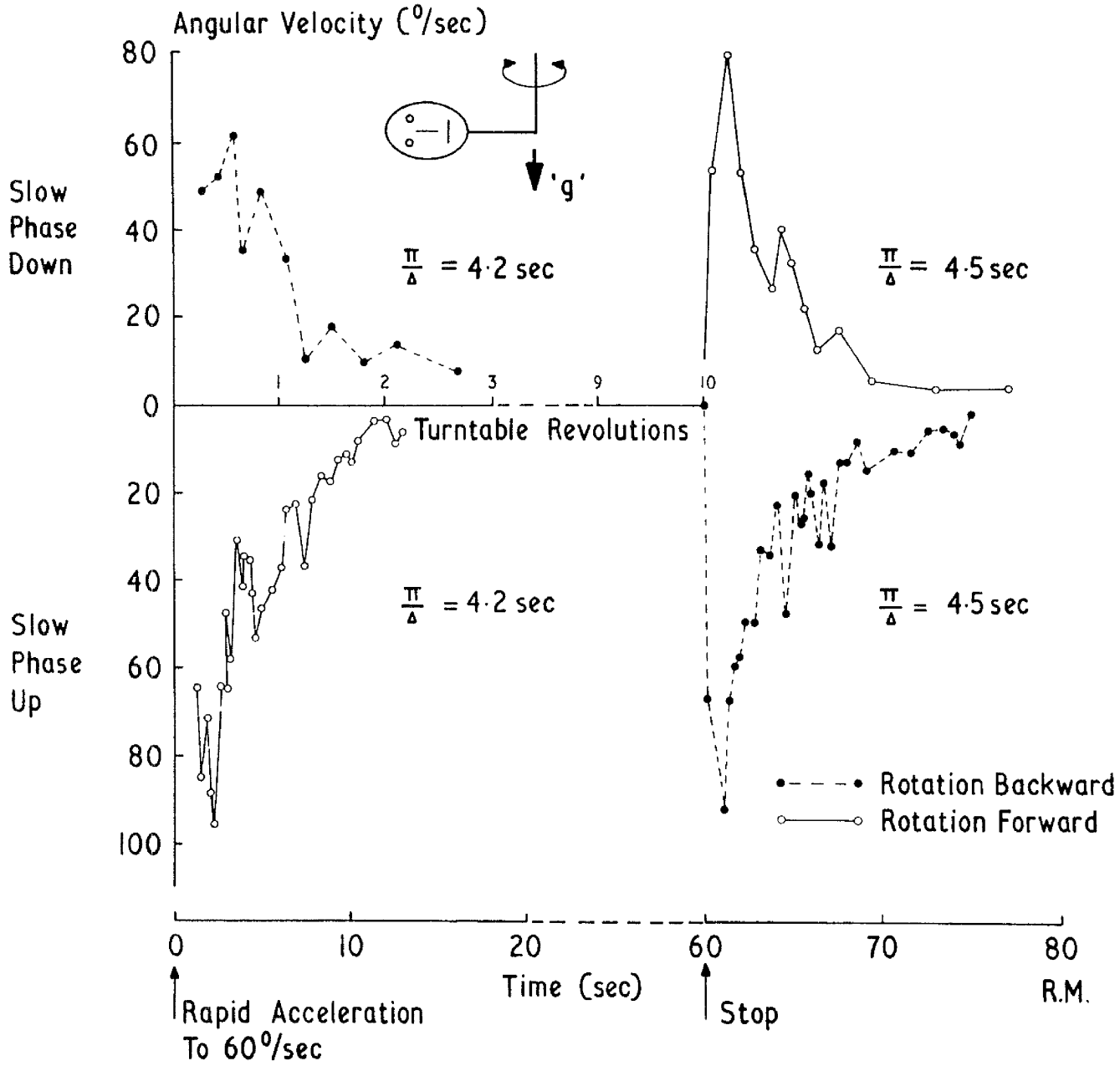


Figure 4.23

Plots of slow phase velocity of vertical nystagmus against time, for one subject, during and after rotation in pitch at 60°/sec about a vertical axis in forward and backward directions. Rotation commenced and terminated (after 10 revolutions) with an impulsive acceleration. The time constants of decay of per-rotational nystagmus (π/Δ 4.2 sec) did not differ significantly from those of post-rotational nystagmus (π/Δ 4.5 sec).

deceleration with the subject in the vertical position. Calibration eye-movements were recorded between successive runs.

Each subject experienced two consecutive runs at 60°/sec, one in each direction of rotation. Five of the subjects commenced with forward rotation, and five with rotation in the backward direction.

RESULTS

Rotation in Pitch about a Vertical Axis

The pattern of per-rotational responses was similar to that observed for rotation in yaw about a vertical axis (Part 3 (2)). All of the subjects stated that their sensations of turning passed off within the first 2-3 revolutions. Only eight subjects, however, produced adequate measurable per-rotational nystagmus, and the record from one of these is shown in Fig 4.22. The nystagmus records were analysed quantitatively (Appendix 1A), and the slow phase velocity of each beat plotted on a linear scale against time from commencement of rotation, for each of the subjects. Fig 4.23 is a plot made in this way from the records of the subject depicted in Fig 4.22. Following acceleration to 60°/sec,

the nystagmus decayed in an exponential manner (c.f. Fig 3.4), until it was no longer discernible after about 3 revolutions (18 sec).

Individual log-linear plots of slow phase velocity against time were also made, in the manner previously described (Part 4, Section 1), and from these the time constant of decay of per-rotational nystagmus, and initial slow phase velocity (ω_{to}), were determined for each of the eight subjects, for both directions of rotation (Appendix 1B). There was no significant difference between the time constants and initial slow phase velocities in the two directions. Accordingly the results for forward and backward rotation were combined. The mean values for each subject are assembled in Table 4.1, and compared with corresponding data for the first three revolutions when the same subjects were rotated in pitch about a horizontal axis (see below); and in yaw about a vertical axis.

Rotation in Pitch about a Horizontal Axis

Subjective experiences

Each subject experienced continuous sensations of turning in a vertical sagittal plane, throughout the period of rotation, in contrast to the rapid disappearance of sensations when the rotation axis was vertical. None of the subjects enjoyed the procedure, however, and rotation in the backward direction was generally found to be distinctly "more unpleasant"

TABLE 4.1

Subject	PITCH (Vert. axis)		PITCH (Horiz. axis)		YAW (Vert. axis)	
	π/Δ	ω_{to}	π/Δ	ω_{to}	π/Δ	ω_{to}
1	4.2	123.0	8.3	100.0	9.3	42.0
2	4.2	77.0	10.4	99.0	6.5	58.3
3	-	-	28.2	71.0	11.6	51.0
4	9.7	32.0	-	-	12.3	32.7
5	14.6	45.0	-	-	10.0	47.2
6	10.8	149.0	12.5	47.0	11.0	43.4
7	9.1	43.0	10.3	96.0	10.9	67.5
8	-	-	6.0	76.5	11.7	47.5
9	12.4	53.0	-	-	16.0	48.5
10	8.3	36.0	-	-	11.7	35.0
Mean	9.2	70.0	12.6	81.7	11.2	47.4

Comparison of the time constant of decay (π/Δ sec) and initial slow phase velocity (ω_{to} °/sec) of per-rotational nystagmus for those subjects who produced measurable records during rotation in pitch about vertical and horizontal axes, and in yaw about the vertical axis. Each value is the mean for rotation in clockwise and counter-clockwise directions.

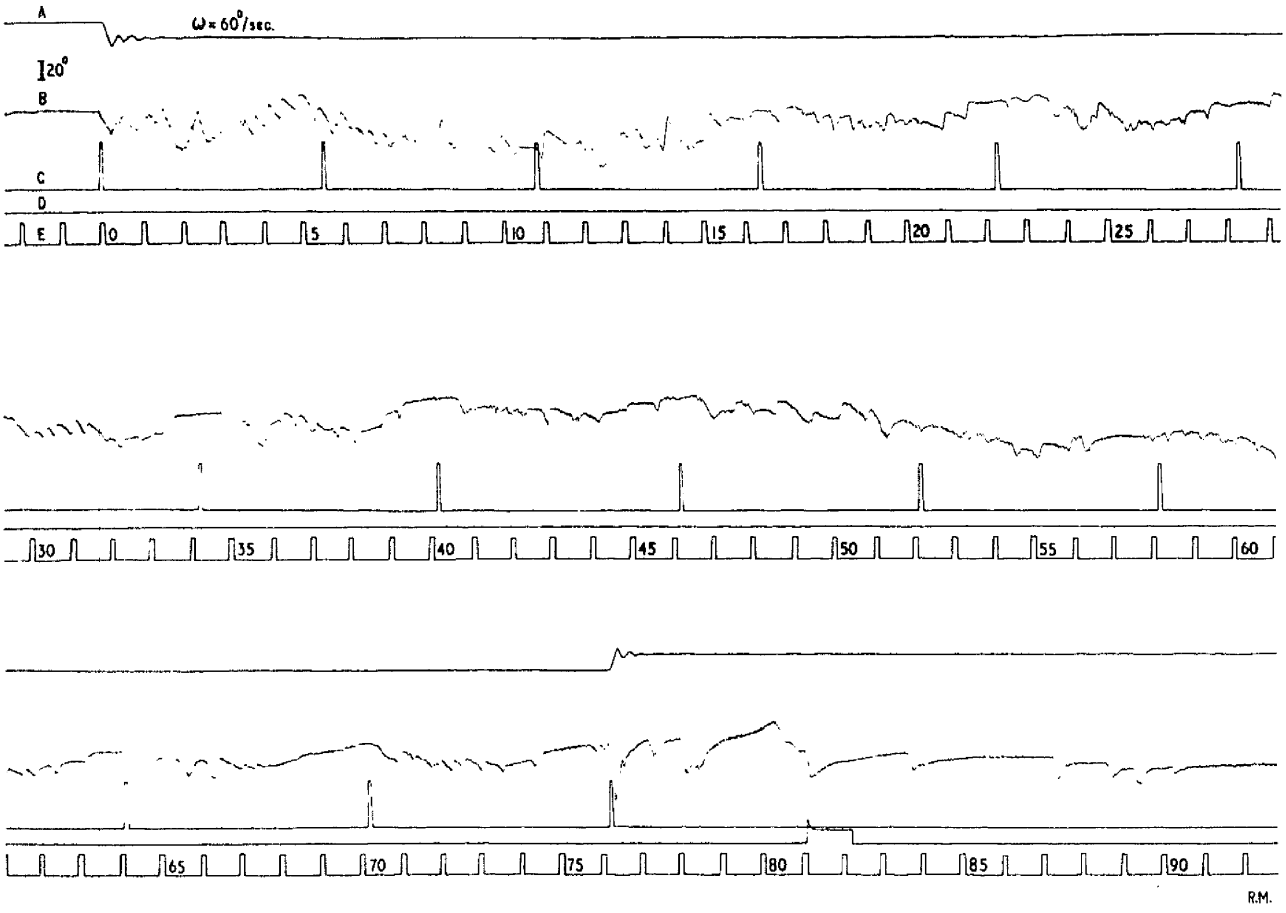


Figure 4.24

Record of vertical eye-movements recorded during and after forward rotation in pitch at 60°/sec about a horizontal axis. The traces are: A tachogenerator signal; B eye-movements; C subject's position - spikes indicate completion of each revolution, when the subject was vertical; D subject response marker; E 1 sec time marker. Rotation commenced at t=0 and ended at t=76 sec.

than forward rotation. Four potential subjects declined to complete their runs because of nausea, and had to be replaced. Six of the subjects who did complete the experiment were nauseated by the end of their session, and one vomited after being released from the chair.

Per-rotational eye-movements

Only six subjects produced adequate per-rotational vertical nystagmus, in contrast to the eight subjects who showed measurable nystagmus when the rotation axis was vertical, and the adequate lateral nystagmus which was present on the records from all of the subjects when they were rotated in yaw about a vertical axis.

In general the per-rotational nystagmic response was similar to that described in the previous section for rotation in yaw about a horizontal axis (Hixon & Niven, unpublished observation ; Bodin, 1968). Fig 4.24 shows a typical record of the vertical eye-movements obtained from one subject during forward rotation at 60°/sec. There was no apparent anti-compensatory eye-movement at the commencement of rotation, as observed in the previous experiment, but instead compensatory nystagmus developed immediately, and was found to persist for as long as rotation continued. This was in contrast to the decay and disappearance of nystagmus within 3 revolutions when the rotation axis was vertical, described above, although

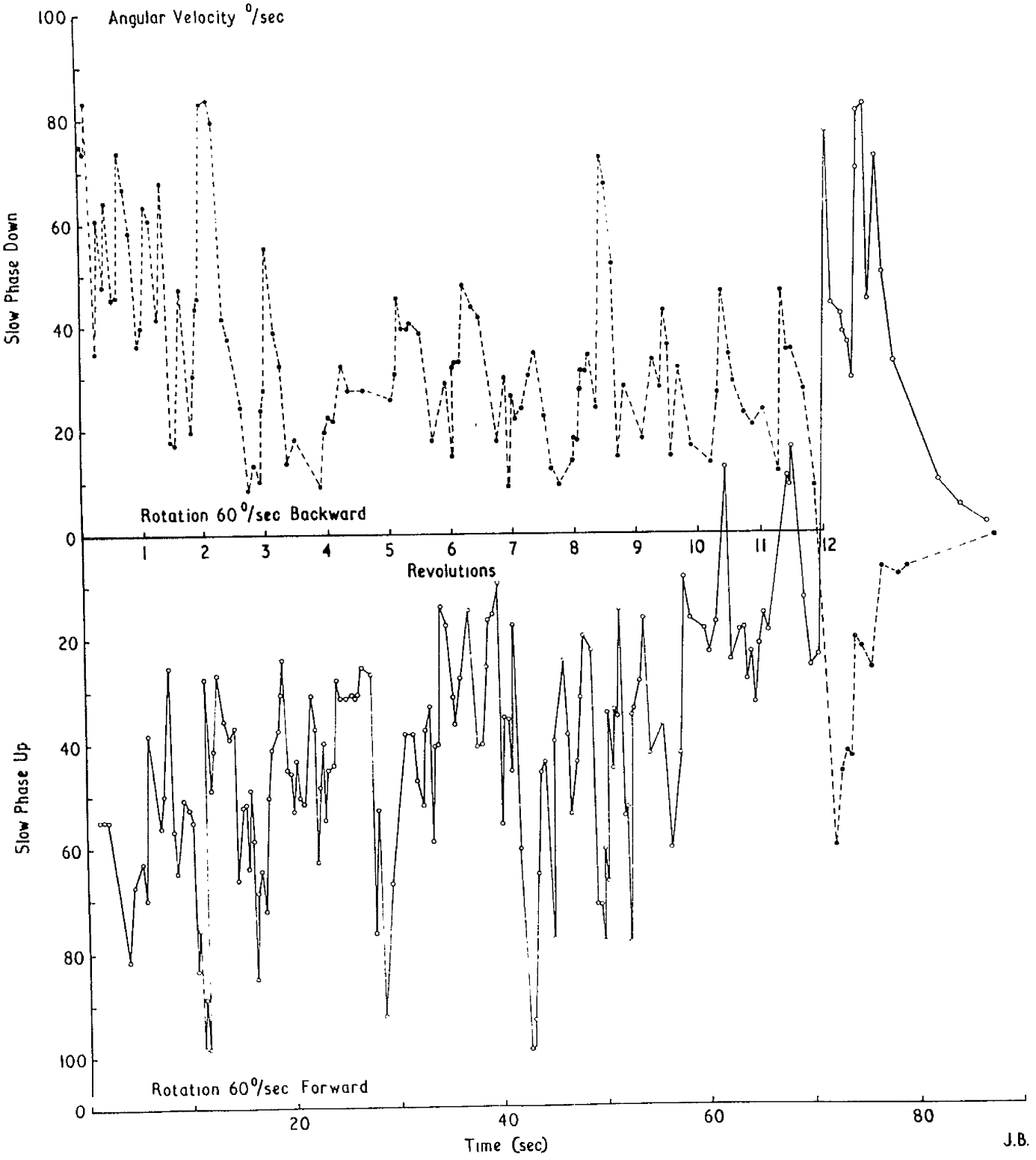


Figure 4.25

Plot of slow phase velocity of vertical nystagmus against time, for one subject, during and after rotation in pitch at 60°/sec about a horizontal axis in forward and backward directions. Rotation commenced and terminated with an impulsive acceleration.

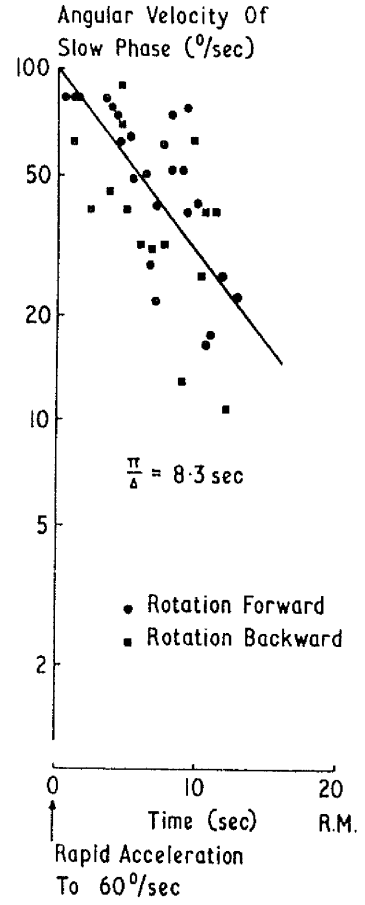


Figure 4.26

Pattern of decay and time constant of per-rotational nystagmus (π/Δ) for one subject during the first 3 revolutions in pitch about a horizontal axis, following impulsive acceleration to 60°/sec. Velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale.

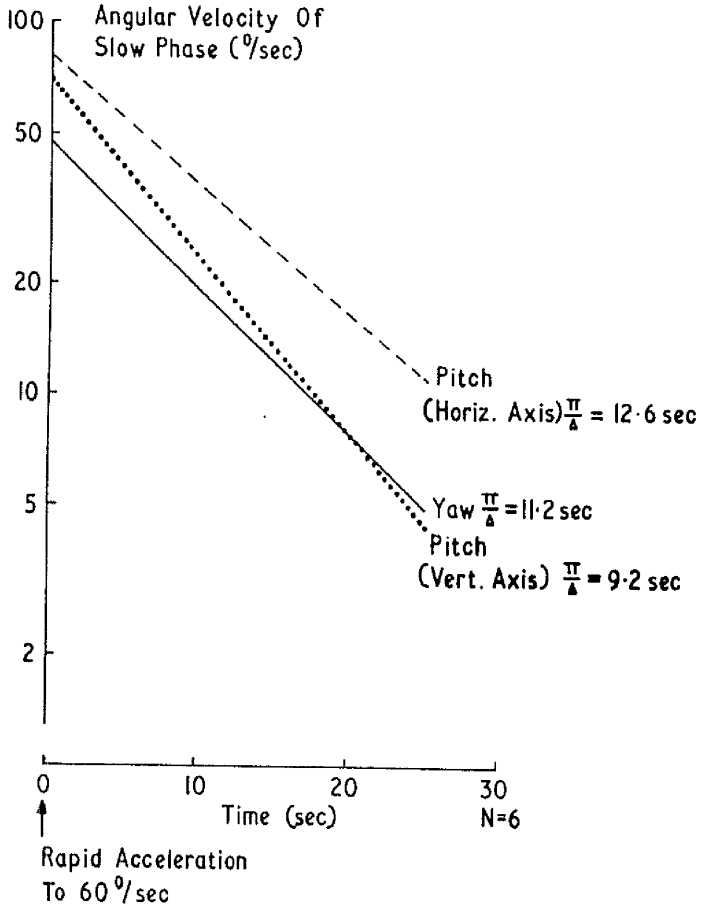


Figure 4.27

Comparison of the mean pattern of decay and time constant of per-rotational nystagmus (π/Δ) during the first 3 revolutions at 60°/sec in the different experimental situations. Slow phase nystagmus velocity is plotted on a logarithmic ordinate scale.

the plane of angular acceleration through the head was the same in each situation. The eye-movement records were analysed quantitatively in the manner already described, and linear plots of slow phase velocity of per-rotational nystagmus against time, for 12 revolutions in the forward and backward directions made for each subject (Fig 4.25). Following initial acceleration, the velocity of slow phase nystagmus decayed in an approximately exponential manner to about one third its initial value, during the first 2-3 revolutions. Thereafter a 'steady-state' condition was established in which, as in the previous experiment, the velocity of sustained nystagmus was modulated according to the position of the subject, although the mean slow phase velocity remained fairly constant.

Four of the subjects showed occasional reversal of nystagmus during their period of rotation (e.g. Fig 4.25 in the last two cycles of forward rotation), but this was not a consistent finding, and in general the nystagmus continued to beat in a compensatory manner throughout, with only irregular and infrequent changes of direction.

Individual log-linear plots of nystagmus slow phase velocity against time, for the first three revolutions, were made (Fig 4.26) as described above, and from these the time constant of decay and initial slow phase velocity of the

per-rotational nystagmus were determined for each subject (Table 4.1, ~~see back~~). The mean patterns of decay of per-rotational nystagmus in the three experimental situations are also shown graphically in Fig 4.27. Analysis of variance did not reveal a significant difference between the time constants for rotation in pitch about the vertical axis (mean 9.2 sec) and horizontal axis (mean 12.6 sec). However this was probably due to the small size of the sample, for only four subjects produced adequate nystagmus in both the vertical and horizontal axes, and it is interesting that for each of these the time constant was longer when the rotation axis was horizontal than when it was vertical (Table 4.1). For rotation in yaw, the time constants (mean 11.2 sec) did not differ significantly from those obtained in pitch.

To investigate the behaviour of the sustained nystagmus with respect to time and position, once 'steady-state' conditions had been established, ten cycles from the second to the thirteenth on the records from each subject were analysed in the manner described in the previous section, and the average pattern of nystagmus slow phase velocity during one cycle of rotation (angular displacement of the subject through 360°) was obtained (Fig 4.29 a & b).

As in the previous experiment, per-rotational nystagmus was characteristically superimposed on slow cyclical swings in potential, irrespective of the direction of rotation (Figs 4.24

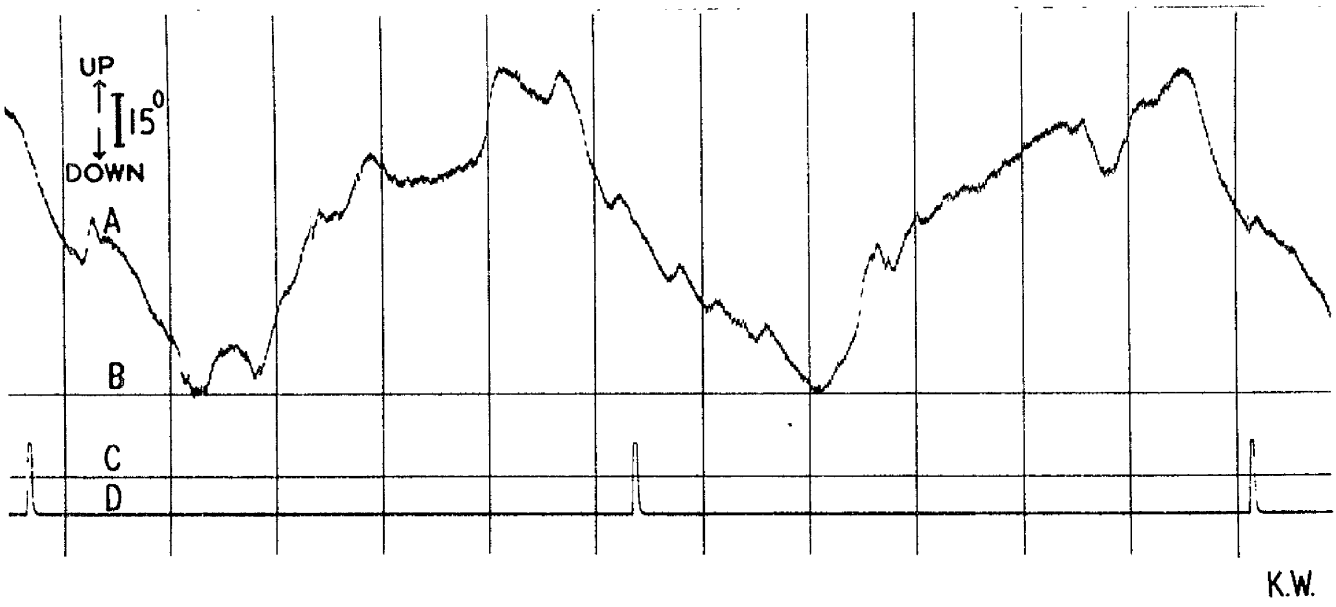


Figure 4.28

EOG record from one subject during 2 cycles of continuous rotation in pitch at 60°/sec about a horizontal axis. The traces are: A EOG; B, C not in use; D subject's position - spikes indicate completion of each revolution, when the subject was upright. Vertical time markers are at 1 sec intervals. Note large amplitude swings of EOG trace and the poor quality of superimposed nystagmic eye-movements.

and 4.28). However, in contrast to the earlier experiment, it was notable that for the majority of subjects the quality of the nystagmic response was inversely related to the amplitude of these swings. Subjects who produced good nystagmus generally showed low amplitude swings (Fig 4.24), while large swings were usually associated with minimal or intermittent nystagmus (Fig 4.28). A number of subjects, not included in the main experiment, produced very large amplitude swings with no nystagmus at all.

It was again not possible to establish with certainty whether these potential changes were a manifestation of eye-movements, or artifacts, but it was necessary as in the previous experiment to correct the measures of slow phase velocity obtained from the records (Fig 4.29), by addition or subtraction of the equivalent angular velocity component of the potential swing on which the nystagmus was superimposed.

The records were analysed with an OSCAR trace-measuring instrument, in the manner previously described, and mean displacement curves for each subject, in both directions of rotation, determined. The six subjects who produced adequate nystagmus were also found to share essentially the same pattern of potential swings, and the individual curves for these subjects were averaged to give the mean displacement curves depicted in Fig 4.30. These curves were then differentiated geometrically, to obtain the corresponding

(a) Cartesian coordinates (plotted over 2 cycles)

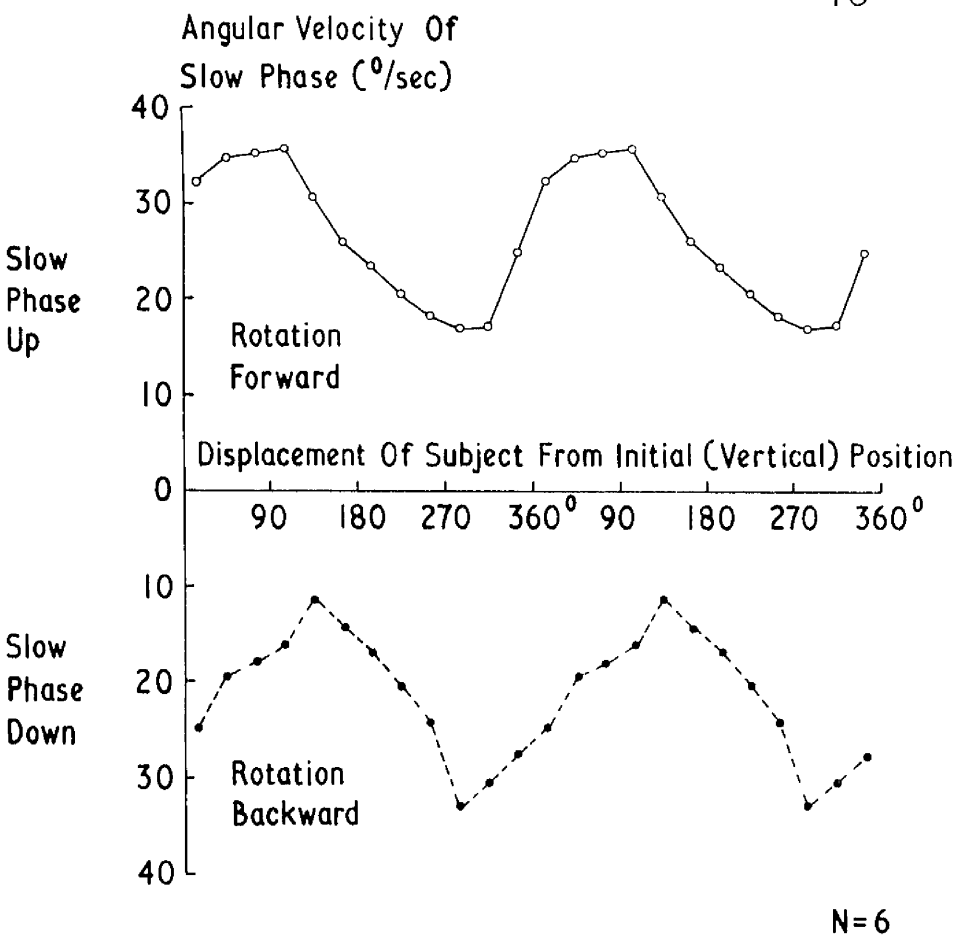
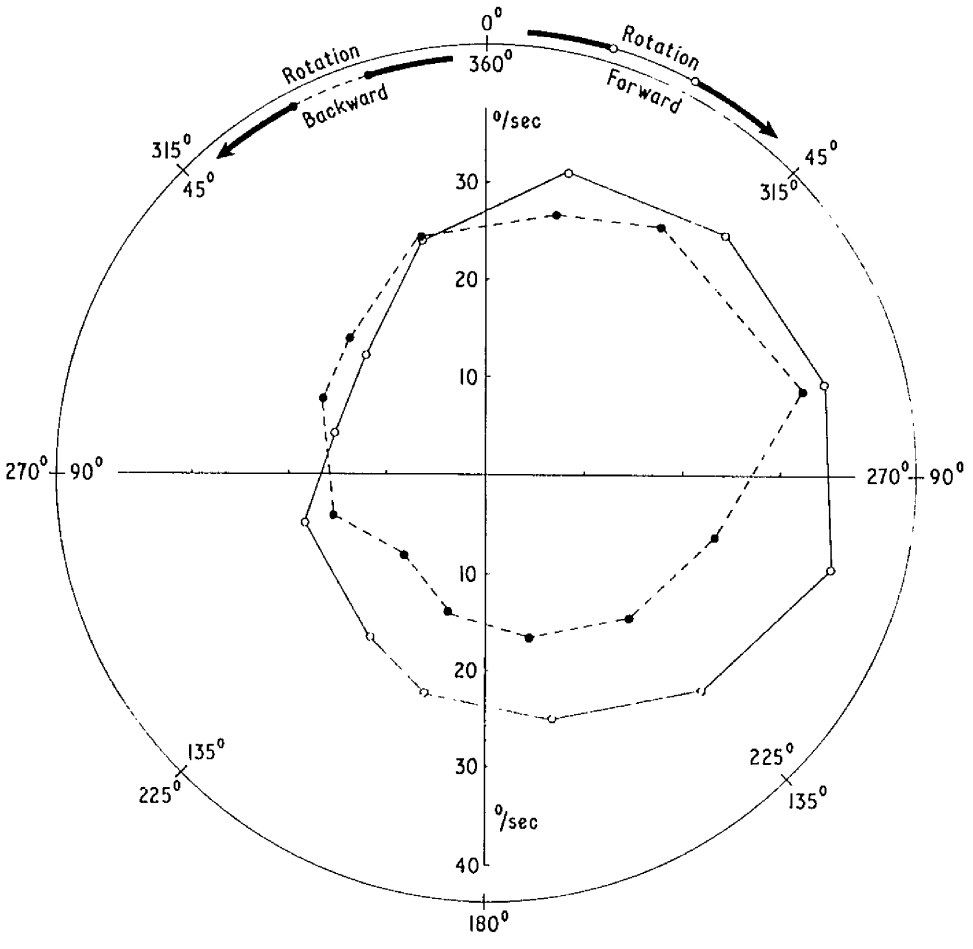


Figure 4.29

Mean plots, in cartesian and polar coordinates, of slow phase velocity of per-rotational nystagmus against subject position, for forward and backward rotation at 60°/sec. Based on results from 6 subjects. Each point is the average velocity, over 10 cycles, of the nystagmus which occurred in each 30° arc. At 0° (360°) subjects were upright, at 180° inverted.



(b) Polar coordinates.

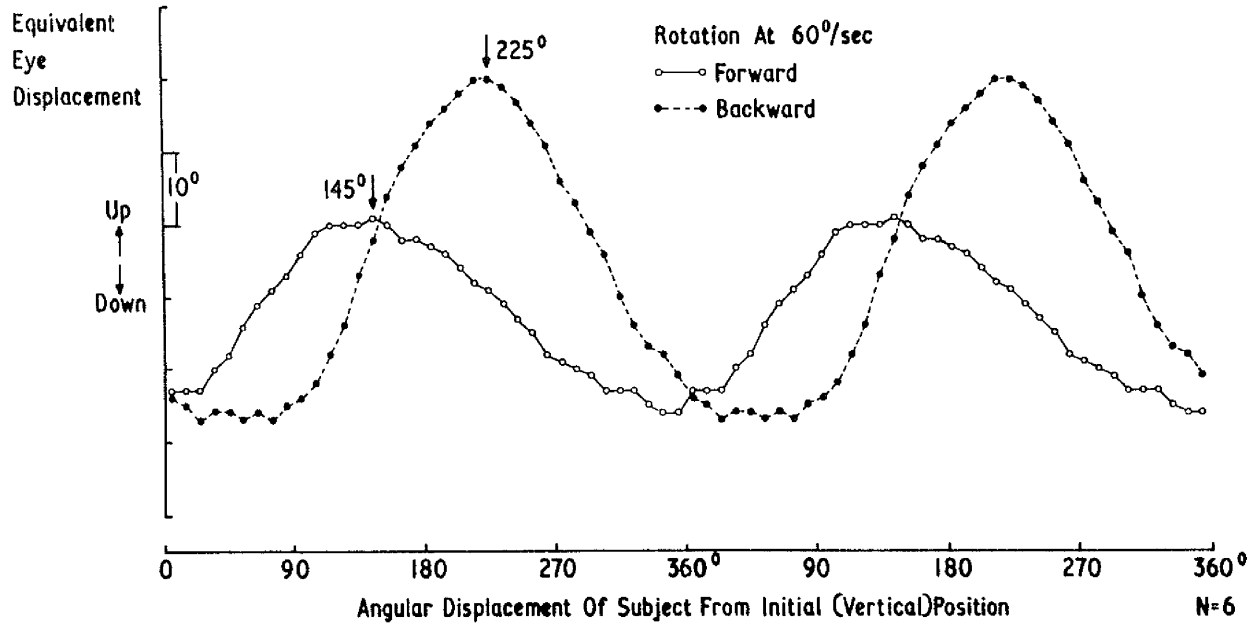


Figure 4.30

Mean pattern of potential swings on which nystagmus was superimposed, for forward and backward rotation, plotted as equivalent eye-displacement against subject position. Each curve, which is plotted over 2 cycles, is the average for 10 rotations in 6 subjects.

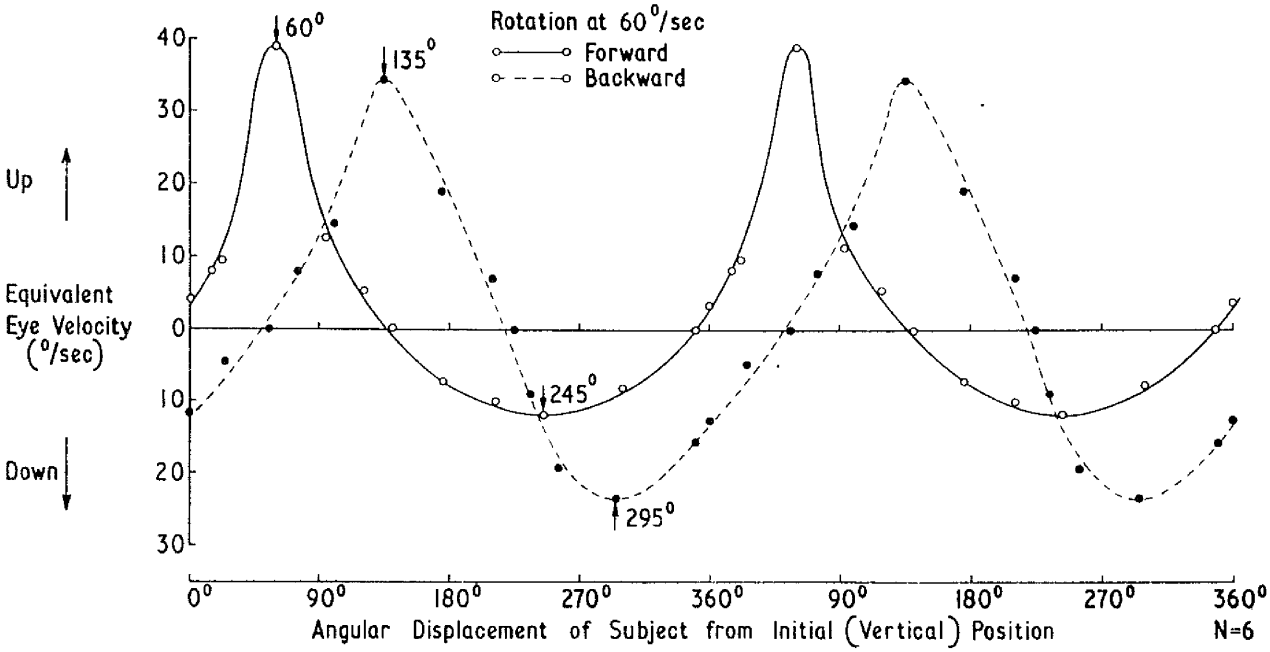


Figure 4.31

Mean curves depicting equivalent eye angular velocity during forward and backward rotation (plotted over 2 cycles) derived from the equivalent eye-displacement curves in Fig 4.30.

curves for equivalent eye angular velocity during forward and backward rotation (Fig 4.31), and the appropriate corrections to be applied in order to obtain true slow phase angular velocity determined.

Correction of the slow phase velocity in this manner altered the form of the plot of nystagmus velocity against subject position, from the pattern in Fig 4.29(b), to that shown in Fig 4.32. From comparison of the graphs of corrected nystagmus velocity against position, for backward and forward rotation (Fig 4.32) it can be seen that while the amplitude of modulation was greater for rotation backward than forward, the pattern of modulation of slow phase velocity was related to the absolute orientation of the subject to the gravitational vertical, irrespective of the direction of rotation, i.e. maximum slow phase velocity occurred when the subject was in the same position each time, corresponding to forward rotation through 225°, or rotation backwards of 135°. This was in contrast to the 'rotating stretcher' experiment, in which the pattern of modulation was symmetrical for the two directions of turning (Fig 4.8), and related only to the angular displacement of the subject from the initial (supine) position.

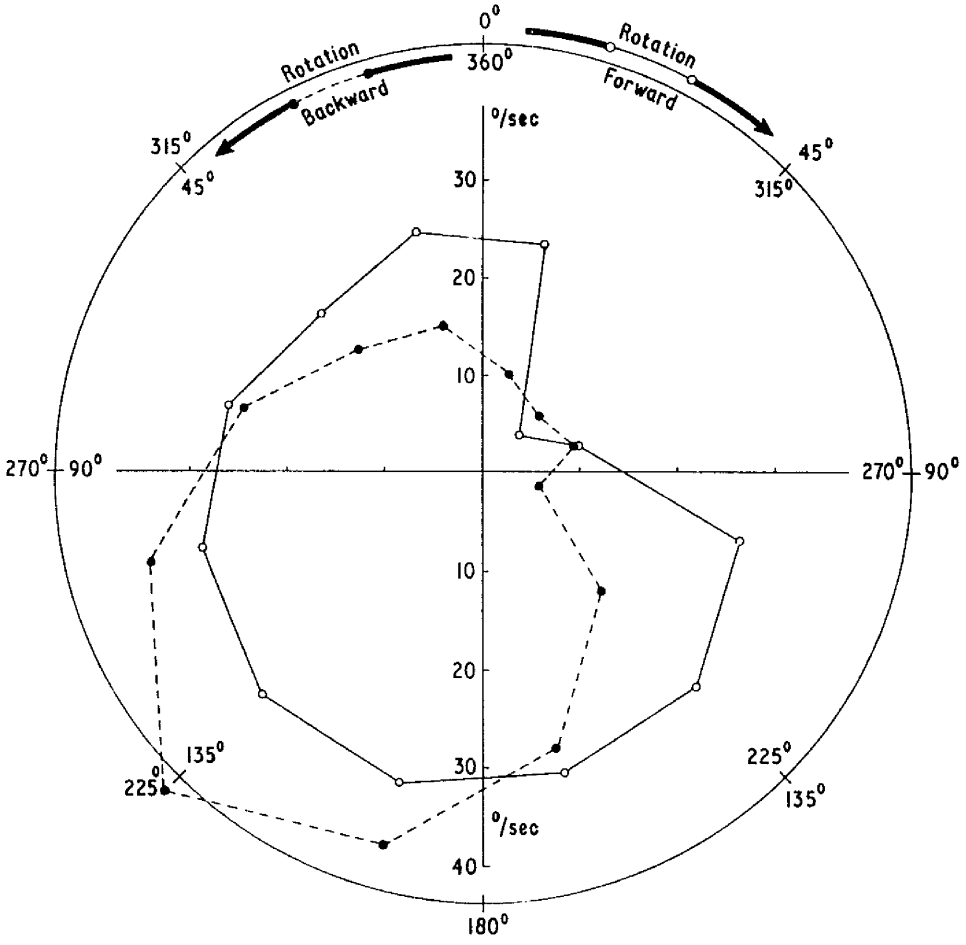


Figure 4.32

Plot in polar coordinates of mean corrected slow phase nystagmus velocity against subject position, for forward and backward rotation at 60°/sec. Other details as in Fig 4.29.

SUMMARY

Rotation in pitch about a horizontal axis was found to produce compensatory vertical nystagmus for as long as rotation continued, which was not present when the same angular stimuli were applied about a vertical axis. The slow phase velocity of nystagmus showed a cyclical modulation, related to the orientation of the subject to the gravitational vertical irrespective of the direction of rotation, though the amplitude of modulation was greater for rotation in the backward than the forward direction.

The findings are in general agreement with those of the previous experiment, and indicate a similar difference in the pattern of responses to angular stimuli about vertical and horizontal axes in pitch (vertical canals) as observed for rotation in yaw (lateral canals).

The results will be discussed in Part 6, together with those of the previous section, and hypotheses presented and compared which attempt to explain the findings either in terms of an alteration in the dynamic behaviour of the canal-cupula-endolymph system mediated by a direct action of the linear (gravitational) acceleration on the end-organ ('g on canal' mechanism, Benson and Bodin, 1966), or by a central process in which

afferent signals from otolith and other gravi-receptor organs interact with those from the semicircular canals ('somaesthetic inhibition', Guedry, 1964). It seems probable, however, on the basis of recent studies conducted in other laboratories that the latter hypothesis is the most likely, though there is still insufficient evidence to enable the possible additional influence of the efferent innervation to ampullary receptors to be assessed.

PART 5

POST-ROTATIONAL VESTIBULAR RESPONSES

PART 5

Section 1

The Effect of Orientation to the Gravitational Vertical on Vestibular Responses Following Rotation in Yaw about a Horizontal Axis

SECTION 1

THE EFFECT OF ORIENTATION TO THE GRAVITATIONAL VERTICAL ON VESTIBULAR RESPONSES FOLLOWING ROTATION IN YAW ABOUT A HORIZONTAL AXIS

Purpose of Experiment

This experiment formed the second part of the investigation of lateral (horizontal) canal function, in which the pattern of responses to angular stimuli in yaw about a horizontal axis (gravitational vector in the transverse plane of the skull), was compared with the responses obtained for rotation in yaw about a vertical axis (g-vector normal to that plane) (Fig 4.1).

The experiment was performed using the rotating stretcher apparatus already described (Part 4, Section 1 (Fig 4.2)), and designed on the basis of preliminary observations of post-rotational responses obtained during the conduct of that experiment, as well as the findings of recent investigations (Guedry, 1964; Correia & Guedry, 1964), carried out concomitantly with the earlier 'rotating stretcher' experiment. These studies showed that following rotation about a horizontal cephalo-caudal body axis, post-rotational responses (both sensations and intensity of nystagmus) were greatly reduced in

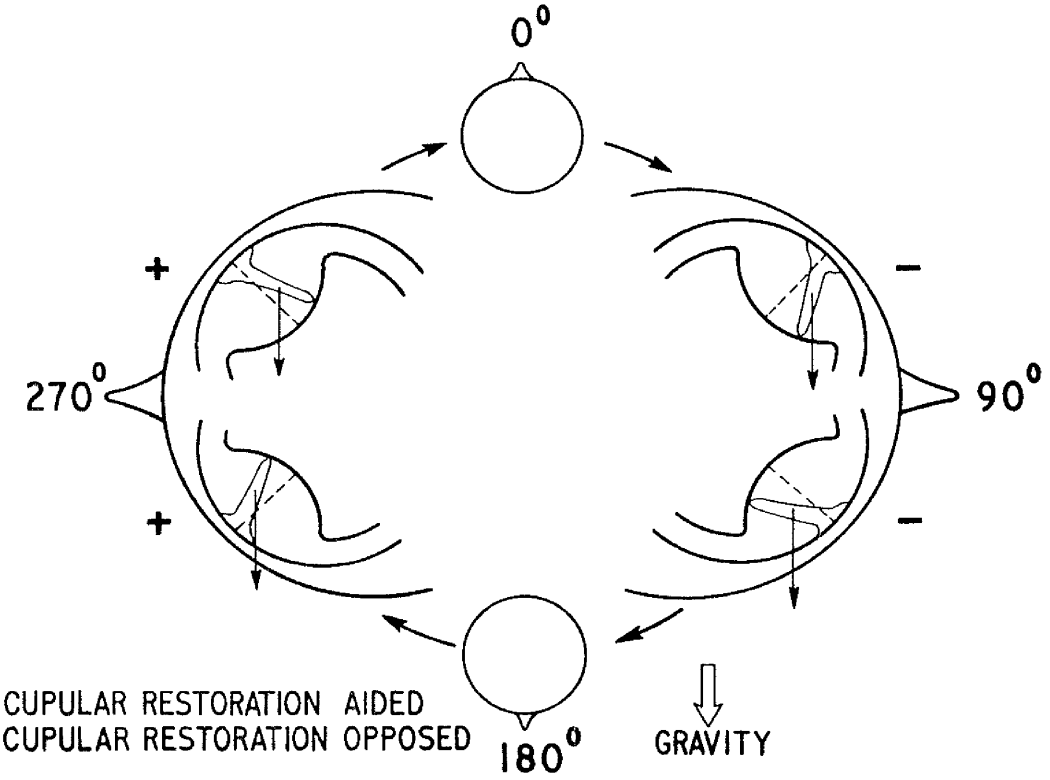


Figure 5.1

Diagrams showing orientation of the head to the gravitational vertical in 4 orthogonal positions when the axis of rotation was horizontal. Direction of rotation was clockwise. During rotation there was modulation of nystagmus velocity, with a minimum at 90° and maximum near the 270° position (Part 4, Section 1, Fig 4.13).

In the present experiment post-rotational responses were examined in each of these 4 positions. Enlarged diagrams show the post-rotational deflection of the cupulae in the 90° and 270° positions, and also the direction of hypothetical forces acting on the cupulae (vertical arrows) which could explain the per-rotational modulation of nystagmus velocity in these positions (assuming it was cupular in origin). If these forces also persisted during the post-rotation period, their effect on cupular behaviour would be as indicated - deflection increased and cupular restoration opposed (ω_{to} maximum and time constant prolonged) in the 90° position, compared with the 270° position, where deflection would be reduced and cupular return assisted (ω_{to} minimum, time constant reduced). In the 0° and 180° positions the effect of these forces would be similar, cupular restoration on one side being aided and on the other opposed in each situation, so that no differences would be expected between post-rotational responses in these positions.

comparison with those evoked by the same angular stimulus when the rotation axis was vertical.

In addition, the sinusoidal modulation of the slow phase velocity of nystagmus during horizontal axis rotation (Part 4, Section 1), according to the position of the subject (Figs 4.13 and 4.16), suggested that the pattern of decay of post-rotational nystagmus might also differ according to the orientation of the head to the gravitational vertical when rotation was stopped. For if this per-rotational nystagmus was a manifestation of cupular deflection, then it might be expected that post-rotational nystagmus, produced by deflection of the cupula in the opposite direction, would be reduced, in comparison with the vertical axis response, by an amount equal to the velocity of the per-rotational nystagmus appropriate to the position in which the stretcher was stopped, i.e. that the initial slow phase velocity of post-rotational nystagmus (ω_{to}) would be maximum in the 90° (right-side-down) position and minimum in the 270° (left-side-down) position. Hypothetical forces acting on the cupula which could produce these changes (if they were cupular in origin) are illustrated schematically in Fig 5.1. Similarly, it might be argued that if these forces persisted during the post-rotation phase, then the rate of cupular return to the resting position would also be affected, with delayed restoration (longer time constant of decay) in the 90° position, compared with the 270° position, as indicated in the diagram.

The observations of Correia and Guedry (1964) suggest that the pattern of post-rotational nystagmus following horizontal axis rotation in yaw differed according to the orientation of the head to the gravitational vertical, but their results were confined to measures of 'nystagmus output' (Part 3, (4)b) so that the relative contribution of velocity and rate (time constant) of decay of nystagmus could not be assessed.

Accordingly the present study was carried out for the purpose of a more detailed examination of the effect of orientation to gravity on the responses following rotation about a horizontal axis. In this experiment the pattern of post-rotational nystagmus (time constant of decay and ω_{to} values) is compared in four orthogonal orientations of the subject to the gravitational vertical (Fig 5.1), and with the responses evoked by the same angular stimulus when the axis of rotation was vertical.

METHOD

The rotating stretcher apparatus and preliminary conduct of the experiment have already been described (Part 4, Section 1, Figs 4.2 and 4.3). In addition, a signalling key was provided

which the subjects were asked to press when their sensation of turning had passed off.

Fourteen laboratory personnel (9 male, 5 female) acted as subjects.

In the earlier experiment it was shown that nystagmus induced by the initial impulsive acceleration decayed during the first two or three revolutions of the stretcher, before the characteristic pattern of sustained per-rotational nystagmus became established. Accordingly, in the present experiment, rotation at 60°/sec to the right was maintained for five revolutions (30 sec), to ensure that 'steady-state' conditions had been established, before rotation was stopped by an impulsive deceleration ($300^{\circ}/sec^2$) with the subject in one of four orthogonal positions (Fig 5.1) - namely supine (0°), right-side-down (90°), prone (180°) or left-side-down (270°). Positional accuracy was $\pm 5^{\circ}$. The subject remained in each position for 30 sec. with their eyes closed, while post-rotational lateral nystagmus and the duration of after-sensations were recorded.

Each subject experienced four runs in the experiment, the order in which the stopping positions were presented being varied according to a random design.

On completion of the main experiment, further 'static' recordings of lateral eye-movements were made for 30 sec with the subjects stationary in each of the four positions, to

determine whether any significant spontaneous or position-dependent nystagmus was present. The rate of angular movement between positions in these procedures did not exceed 10°/sec.

RESULTS

Post-rotational Sensations

As reported by Guedry (1964), and noted during the earlier 'rotating stretcher' experiment (Part 4, Section 1), the illusory sensations of turning following rotation in yaw about a horizontal axis were very short indeed, compared with the duration of after-sensations (15-25 sec) when the same angular stimulus was applied about a vertical axis. These findings were confirmed in the present experiment.

For the majority of subjects after-sensations of turning, beyond the sudden jar of stopping, were virtually absent, or of such short duration that they could not be recorded with accuracy. Only three subjects consistently reported measurable after-sensations, and the mean duration of these sensations in all horizontal positions was 4.9 sec. The mean duration of after-sensations for these subjects in the vertical axis was 18.5 sec. It was therefore not possible to draw any conclusions about differences in the duration of sensations in the four horizontal positions. Similarly, the subjective assessments

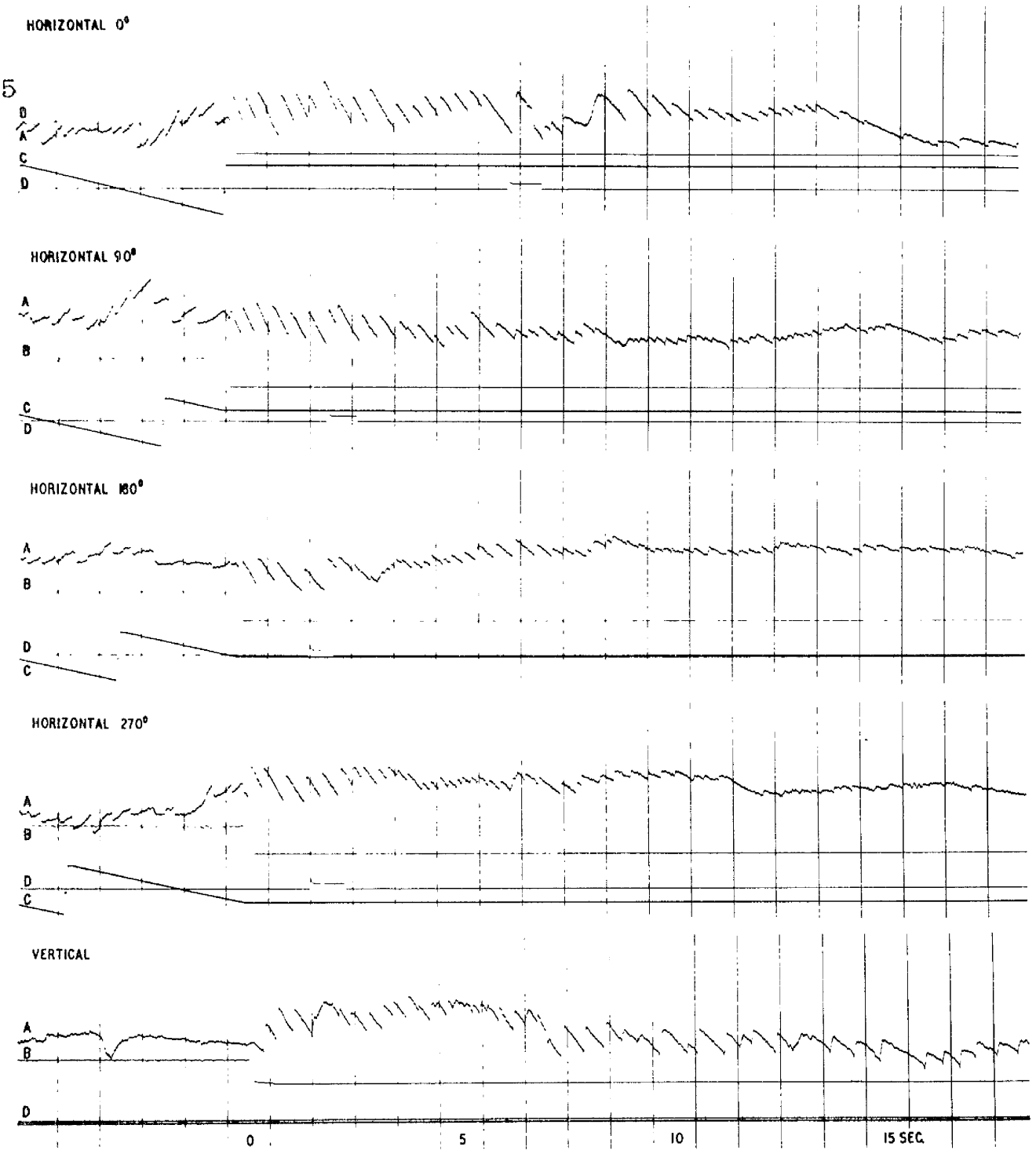


Figure 5.2

Records of post-rotational nystagmus obtained from one subject in four horizontal positions and when the axis of rotation was vertical. The traces are: A eye-movements, B angular velocity of rotation, C stretcher position, and D subject's response (termination of after-sensations); on the bottom record (rotation axis vertical) the duration of after-sensations exceeded 18 sec. Vertical scale: 4 mm. = 10° lateral eye-movement. Time markers are at 1 sec intervals.

obtained from each subject at the end of the experiment did not reveal any consistent differences according to the position in which they were stopped.

None of the subjects experienced nausea in this experiment, as in the earlier 'rotating stretcher' experiment (Part 4, Section 1). This was probably because in the present procedure rotation was continued for a relatively short period (30 sec) only.

Post-rotational Nystagmus

Typical records of post-rotational nystagmus obtained from one subject in the four stopping positions, and when the axis of rotation was vertical, are shown in Fig 5.2. Characteristically, when rotation of the stretcher was stopped, the per-rotational nystagmus with slow phase to the left was immediately replaced by nystagmus in the opposite direction, which subsequently decayed in an approximately exponential manner. From inspection of the records it can be seen that the duration of nystagmus was shorter and the rate of decay more rapid following horizontal axis rotation, than when the rotation axis was vertical, although there is no appreciable difference in the frequency or amplitude of nystagmus in the various situations.

The records from eleven of the subjects contained well defined nystagmus in all stopping positions, but in the remaining three subjects the post-rotational response in one or

TABLE 5.1

Subject	0°		90°		180°		270°		Mean Horizontal Axis		Mean Vertical Axis	
	ω_{to}	π/Δ	ω_{to}	π/Δ	ω_{to}	π/Δ	ω_{to}	π/Δ	ω_{to}	π/Δ	ω_{to}	π/Δ
1	45.5	6.4	36.5	6.6	53.5	5.0	-	-	-	-	38.5	16.0
2	37.6	5.3	38.6	13.3	25.0	11.3	-	-	-	-	41.0	27.0
3	12.8	8.1	16.0	7.7	-	-	12.0	6.5	-	-	11.5	24.0
4	17.8	11.7	17.8	12.3	12.5	11.4	18.6	16.3	16.7	12.9	33.0	16.7
5	21.8	7.9	25.2	4.2	13.4	11.7	27.2	4.6	21.9	7.1	36.0	12.8
6	30.0	5.4	58.0	3.2	38.0	6.7	38.5	6.7	41.2	5.5	31.5	12.0
7	45.0	7.3	45.0	7.3	20.0	7.4	24.5	9.6	33.6	7.9	35.0	17.3
8	54.0	6.7	36.0	11.2	42.0	6.7	19.7	16.2	37.9	10.2	50.0	13.8
9	33.3	5.4	31.3	4.3	21.5	3.5	17.2	6.8	25.9	5.0	31.0	12.3
10	38.3	13.4	47.4	8.4	26.0	10.8	27.7	13.3	34.8	11.5	34.0	19.4
11	54.0	8.0	50.7	8.3	44.0	8.0	35.3	8.7	46.0	8.3	44.3	17.8
12	33.5	9.2	42.5	7.7	28.0	7.8	45.0	4.8	37.2	7.4	45.0	11.5
13	18.0	17.5	32.5	10.4	21.4	11.2	21.4	12.4	23.4	12.9	35.4	18.4
Mean	34.6	9.2	37.6	7.7	25.8	8.9	27.9	9.9	31.4	8.9	36.8	16.6

Time constant of decay (π/Δ sec) and initial slow phase angular velocity (ω_{to} °/sec) of nystagmus following rotation about a horizontal and a vertical axis. In the horizontal axis, rotation of the stretcher was stopped in 4 orthogonal positions.

other of the positions was inadequate for quantitative analysis. The failure to obtain adequate nystagmus in these positions was unlikely to have been due to a low 'arousal level' (Collins and Guedry, 1962), for repetition of the stimulus while the subject performed mental arithmetic failed to evoke a better nystagmic response.

The eye-movement records were analysed quantitatively (Appendix 1A), and as the decay of post-rotational nystagmus appeared to follow on exponential time course, the time constant of decay (π/Δ) and initial slow phase velocity (ω_{to}), in each stopping position, were determined in the manner described in Appendix 1B. These values are assembled in Table 5.1. In addition, the average slow phase nystagmus velocity during each 1 sec interval after deceleration was calculated, and the means of these values for the eleven subjects plotted on a logarithmic ordinate scale, against time after stopping, in order to provide a graphical representation of the pattern of post-rotational decay (Fig 5.3).

The values in Table 5.1 were analysed statistically by the methods already described (Part 3 (8)). When the axis of rotation was horizontal, the mean nystagmus time constant (π/Δ 8.9 sec) was appreciably shorter than when the rotation axis was vertical (π/Δ 16.6 sec), and this difference was highly significant ($p= 0.001$). There was no significant difference between the time constants in the four horizontal

positions. Analysis of the ω_{to} values in the horizontal axis showed that these were significantly greater ($p = 0.05$) at 0° and 90° (mean 36.1°/sec) than in the 180° and 270° positions (mean 26.8°/sec). When the rotation axis was vertical, the mean value of ω_{to} (36.8°/sec) did not differ significantly from that observed in the 0° and 90° horizontal axis positions.

The time constants of decay of post-rotational nystagmus in the horizontal axis were also compared with the time constants obtained from the per-rotational nystagmus during the first two cycles of continuous rotation in the earlier experiment (Part 4, Section 1). The mean time constant following rotation about the horizontal axis (8.9 sec) was found to be significantly smaller ($p = 0.01$) than the time constant of per-rotational nystagmus, both in the horizontal axis (17.7 sec) and the vertical axis (17.3 sec).

Relationship between After-sensations and the Slow Phase Velocity of Post-rotational Nystagmus

If the angular velocity of slow phase nystagmus is regarded as an indicant of the afferent vestibular signal (Lorente de Nó, 1933), then the slow phase velocity of post-rotational nystagmus will be related to the intensity of the after-sensations, and the nystagmus slow phase velocity at the moment at which a subject reports the disappearance of these sensations may be regarded as a measure of sensory 'threshold'.

In Fig 5.3 the average sensory 'thresholds', for those subjects who reported measurable after-sensations, have been delineated in this way. When the axis of rotation was vertical, after-sensations persisted until the nystagmus slow phase velocity had fallen to 12°/sec, whereas the corresponding 'threshold' when the rotation axis was horizontal was equivalent to a nystagmus velocity of between 17-18°/sec. This finding suggests that following rotation about a horizontal axis the sensory 'threshold' was raised, compared with the 'threshold' for perception of sensations engendered by the same angular stimulus applied about a vertical axis. It seems likely that this was a manifestation of competition between ampullary signals and those from otolith and other somaesthetic organs, in which there was more rapid inhibition of inappropriate vestibular signals by the relatively greater gravi-receptor input when the rotation axis was horizontal, compared with when it was vertical ('somaesthetic inhibition' mechanism).

Lateral Nystagmus in 'Static' Positions

In all but four of the subjects, lateral (horizontal) nystagmus was present on the 'static' recordings made in one or more of the stopping positions, but in general this was of such low velocity (1 to 3°/sec) that it was unlikely to modify the pattern of post-rotational nystagmus to any appreciable extent. The mean angular velocity and direction

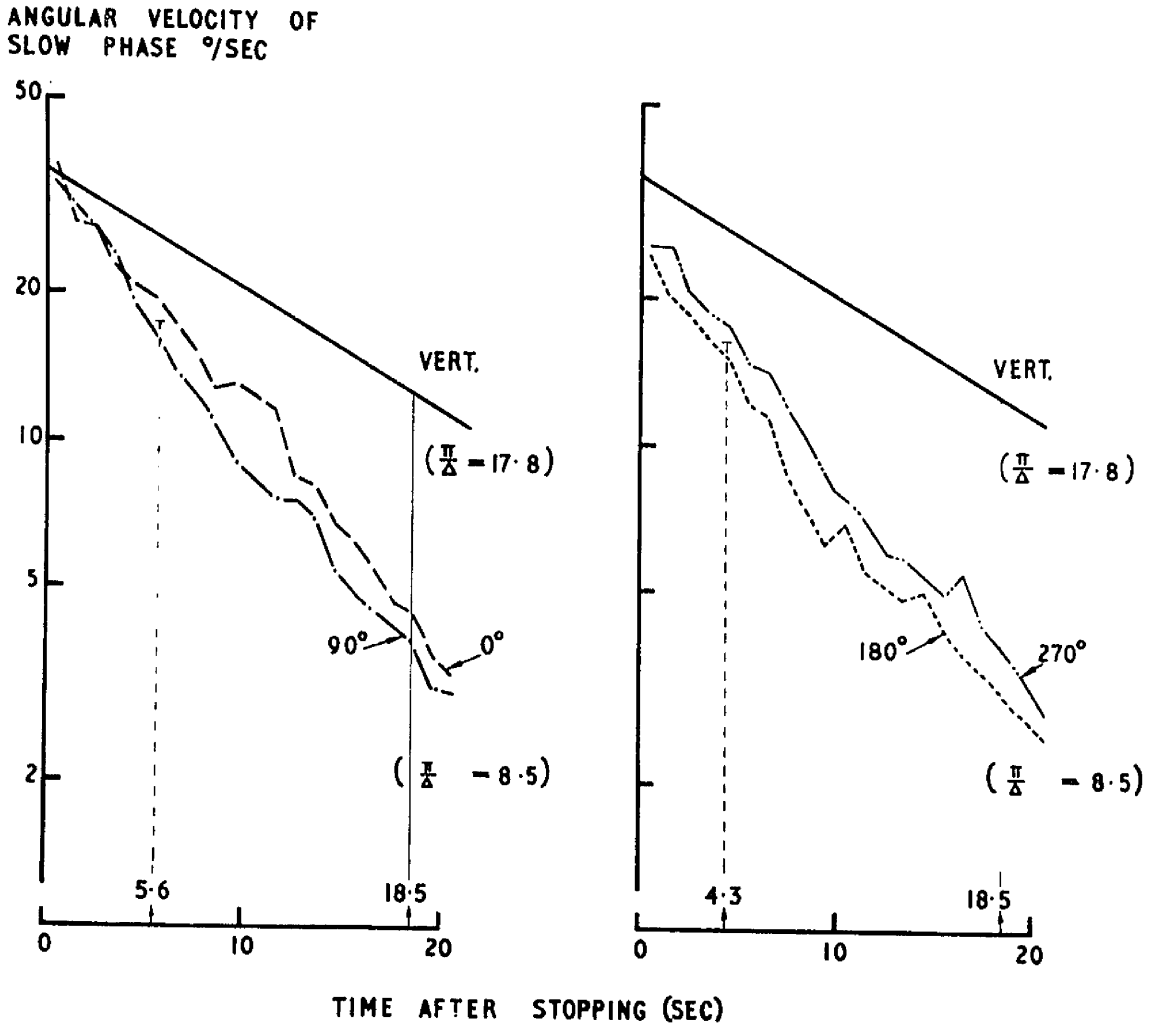


Figure 5.3

Mean decay pattern and time constant of nystagmus (π/Δ sec), in the 4 horizontal stopping positions and when the axis of rotation was vertical, following impulsive deceleration from 60°/sec in yaw (z body axis). Based on results from 11 subjects. Angular velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale. Corresponding durations of after-sensations (sec), for the 5 subjects who reported measurable sensations when the rotation axis was horizontal - average 5.6 sec (0° and 90° positions), 4.3 sec (180° and 270° positions), 18.5 sec (vertical axis) - are indicated on the abscissa by arrows.

of this nystagmus is shown in Table 5.2. In subjects 2 and 3 the direction of nystagmus varied with position, but in the remaining eight subjects it was unidirectional in all positions in which it was present.

SUMMARY

Following rotation to the right at 60°/sec about a horizontal cephalo-caudal axis, the time constant of decay of nystagmus produced by an impulsive deceleration was significantly shorter than when the rotation axis was vertical. The direction of the gravitational acceleration, however, when it lay in the transverse plane of the skull (i.e. approximately coplanar with the stimulated (lateral) canals) had no consistent effect on the time constant of decay, though the initial velocity of post-rotational nystagmus was greater at 0° and 90° than in the 180° and 270° positions.

After-sensations were virtually absent in the horizontal axis, compared with those engendered by the same angular stimulus when the rotation axis was vertical. This was apparently associated with an increase in the sensory 'threshold' following rotation about the horizontal axis.

TABLE 5.2

Subject	Mean Slow Phase Velocity (°/sec) and Direction of Nystagmus in each position				Type of Nystagmus
	0°	90°	180°	270°	
2	2.6 L	1.8 R	2.4 R	3.2 L	Position Dependent
3	0.5 R	1.2 L	-	0.7 R	
4	0.9 R	1.1 R	1.6 R	1.1 R	Spontaneous
5	2.1 R	0.5 R	2.5 R	3.6 R	
6	-	-	1.8 R	-	
7	1.6 L	2.6 L	0.9 L	-	
8	2.1 L	-	-	4.2 L	
11	2.8 R	5.3 R	4.3 R	3.8 R	
12	-	-	1.4 R	-	
14	-	-	-	1.7 R	

Lateral Nystagmus in Different stationary positions

(Subjects not included in this table did not show nystagmus in any of these positions.)

The findings imply that post-rotational responses, following adequate angular stimulation of the lateral canals, depend on the orientation of the subject to the gravitational vector, though not on the direction of the linear acceleration when coplanar with these canals.

The results will be discussed in detail in Part 6.

PART 5

Section 2

Comparison of Vestibular Responses Following Rotation in Pitch about Vertical and Horizontal Axes

SECTION 2

COMPARISON OF VESTIBULAR RESPONSES FOLLOWING ROTATION IN PITCH ABOUT VERTICAL AND HORIZONTAL AXES

Purpose of Experiment

This experiment formed the second part of the investigation of vertical semicircular canal function, in which the pattern of responses to angular stimuli in pitch about a horizontal axis (g-vector in the sagittal plane of the skull, i.e. component of g-vector revolving in the plane of the stimulated canals during rotation) was compared with the responses obtained for rotation in pitch about a vertical axis (no change in orientation of vertical canals to the gravitational vector during rotation) (Fig 4.19).

This section is an account of the post-rotational results obtained during the conduct of the experiment already described in Part 4, Section 2.

The responses following rotation in pitch about a horizontal axis are compared with those obtained for rotation in pitch about a vertical axis, and with the pattern of responses following rotation in yaw about a vertical axis.

TABLE 5.4

Subject	PITCH (Vert. axis)	PITCH (Horiz. axis)	YAW (Vert. axis)
1	17.5	11.2	15.5
2	17.0	7.5	35.9
3	8.2	2.0	12.1
4	24.5	8.2	47.2
5	11.5	7.3	15.1
6	16.8	10.4	27.0
7	17.1	9.1	19.6
8	12.0	5.9	26.0
9	28.0	7.7	51.3
10	5.5	7.0	6.0
Mean	15.8	7.6	25.6

Mean duration of after-sensations (sec), for both directions of rotation, following impulsive deceleration from 60°/sec, in pitch about vertical and horizontal axes, and in yaw about a vertical axis.

METHOD

The apparatus, subjects, and conduct of the experiment have already been described (Part 4, Section 2). After 12 revolutions at 60°/sec about a horizontal axis, in the forward and backward directions, rotation was stopped by an impulsive deceleration with the subject in the vertical position (Fig 4.20). Post-rotational vertical eye-movements were recorded for 30 sec with the eyes closed. Subjects were also instructed to concentrate on their after-sensations of turning, and to press the signalling key when these finally disappeared.

The procedure was similar for rotation in pitch and yaw about a vertical axis on the turntable, except that no special attention was paid to the position in which the turntable was stopped.

RESULTS

Post-rotational Sensations

All of the subjects experienced measurable after-sensations in the three experimental situations. The mean values for each subject are shown in Table 5.4. The after-sensations in yaw (average 25.6 sec) were significantly longer ($p = 0.01$) than

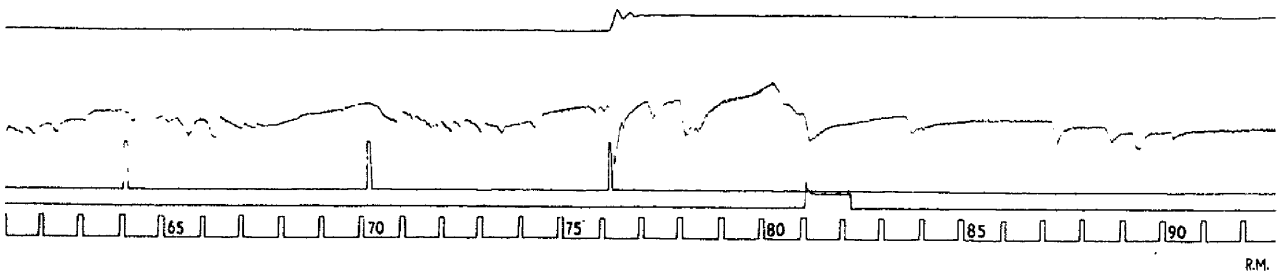


Figure 5.4

Record of vertical eye-movements recorded during and after forward rotation in pitch at 60°/sec about a horizontal axis. From above downward the traces are: tachogenerator signal, eye-movement, subject position indicator, subject response marker, 1 sec time marker. Rotation stopped at t=76 sec. After-sensations terminated at t=81 sec.

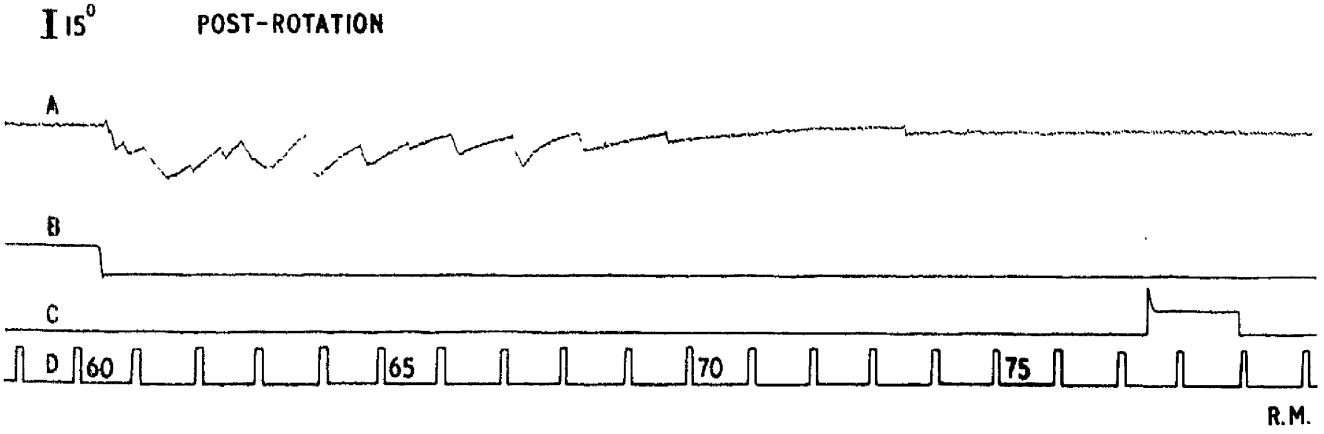


Figure 5.5

Record of vertical nystagmus following forward rotation in pitch at 60°/sec about a vertical axis. The traces are: A eye-movements, B tachogenerator signal, C subject response marker, D 1 sec time marker. Rotation stopped at t=60.3 sec. After-sensations terminated at t=77.3 sec.

those in pitch. When the axis of rotation was horizontal, the duration of sensations in pitch (average 7.6 sec) was significantly shorter ($p = 0.01$) than when the rotation axis was vertical (average 15.8 sec). However, the reduction of after-sensations following stimuli in pitch about the horizontal axis, compared with when it was vertical, was not as great as that recorded for stimuli in yaw in the previous section.

Post-rotational Nystagmus

The post-rotational records from all ten of the subjects contained adequate measurable nystagmus, both in the vertical and horizontal axes. Typical records obtained from one subject are shown in Figs 5.4 and 5.5. It can be seen that when the rotation axis was horizontal (Fig 5.4), on cessation of turning the characteristic per-rotational nystagmus was immediately replaced by nystagmus in the opposite direction, the slow phase velocity of which decayed until nystagmus was no longer discernible after about 15 sec. Comparison of the two records also shows that the quality of the nystagmic response was better following stimuli about the vertical axis, than when the rotation axis was horizontal, although there is no obvious difference, on inspection, between the rate of decay of nystagmus on the two records. None of the subjects showed any significant spontaneous vertical nystagmus.

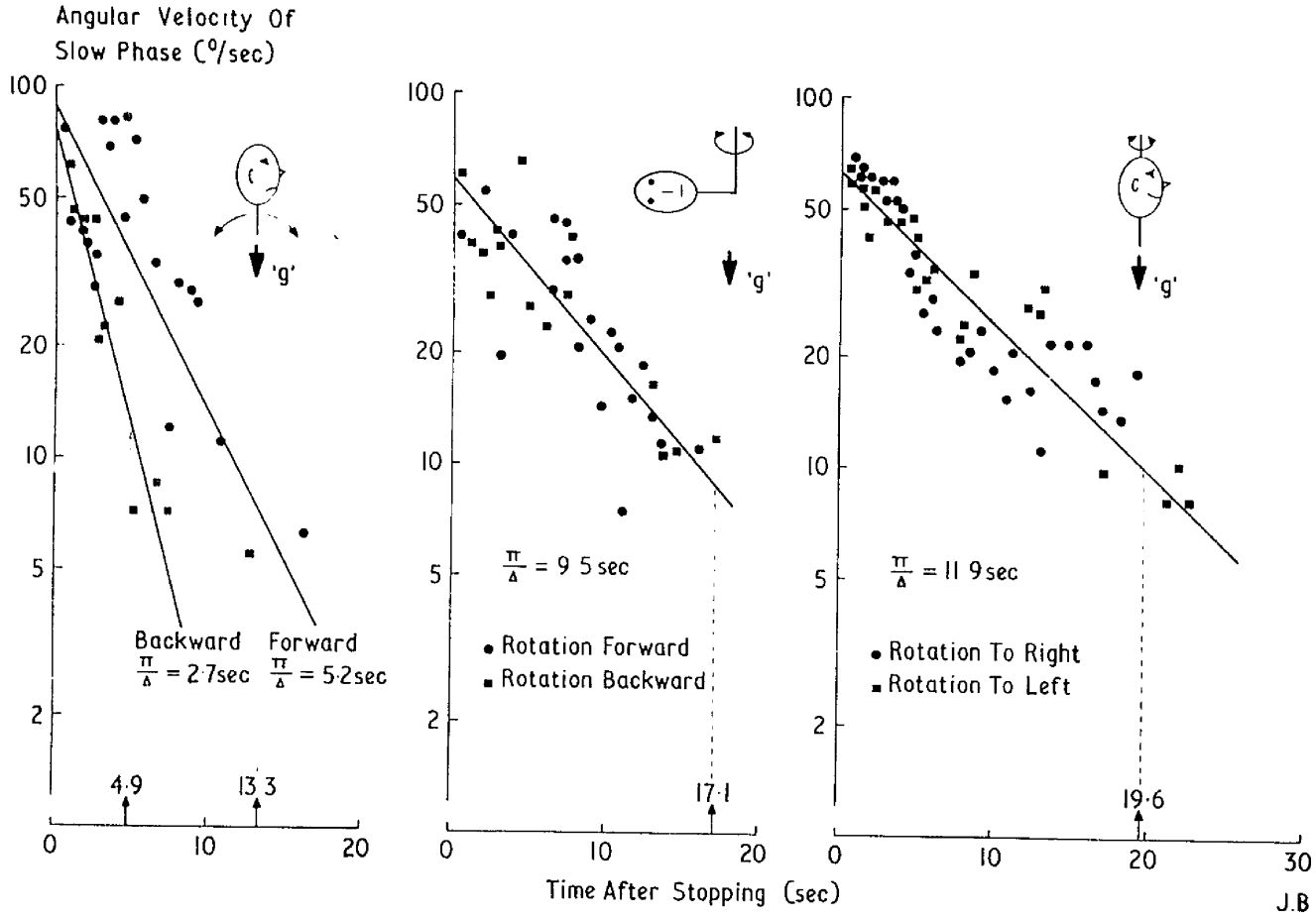


Figure 5.6

Comparison of the pattern of decay and time constant of post-rotational nystagmus (π/Δ sec), in one subject, evoked by impulsive deceleration from 60°/sec in pitch - axis of rotation horizontal (left), vertical (centre) - and in yaw about a vertical axis (right). Angular velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale. Corresponding durations of after-sensations (sec) are indicated on the abscissae by arrows.

The eye-movement records were analysed quantitatively (Appendix 1A), and individual log-linear plots of slow phase velocity against time were drawn for each subject in the manner previously described (e.g. Fig 5.6). From these the time constant of decay (π/Δ) and initial slow phase velocity (ω_{to}) of post-rotational nystagmus were determined (Appendix 1B), for forward and backward rotation, in the three experimental situations (Table 5.5). Analysis of variance of the data in Table 5.5 revealed that when the rotation axis was horizontal, the nystagmus time constant was significantly greater ($p = 0.01$) following rotation in the forward direction (mean π/Δ 14.6 sec) than the backward direction (mean π/Δ 10.9 sec). However, neither of these values differed significantly from the time constant of decay following rotation about the vertical axis in pitch or in yaw. There was also no significant difference in the ω_{to} values, either according to the axis or direction of rotation, or the position of the subject.

In Fig 5.7 the mean patterns of decay of nystagmus in the different experimental situations are shown graphically, and also the average sensory 'thresholds' in each situation, delineated in the manner described in the previous section (i.e. as the slow phase nystagmus velocity corresponding to the time at which after-sensations passed off). As in the previous experiment, it can be seen that the 'threshold' for perception of post-rotatory sensations measured in this way differed both

TABLE 5.5

Subject	PITCH (Vert. axis)		PITCH (Horizontal axis)				YAW (Vert. axis)	
	π/Δ	ω_{to}	π/Δ		ω_{to}		π/Δ	ω_{to}
			F	B	F	B		
1	4.5	90.0	4.7	4.7	59.0	59.0	11.3	38.9
2	7.7	51.7	16.5	5.4	30.0	76.0	13.0	47.0
3	5.0	63.5	45.0	33.0	38.0	41.5	7.2	63.0
4	6.7	50.7	13.5	12.4	81.0	40.0	11.8	39.0
5	9.8	33.8	5.8	4.4	140.0	110.0	21.8	32.5
6	17.8	76.0	9.3	9.5	49.0	36.0	8.8	45.0
7	9.5	58.0	5.2	2.7	88.0	77.0	11.9	61.0
8	7.5	50.0	15.0	10.3	36.0	17.3	19.4	34.0
9	36.4	35.0	15.9	13.8	75.0	22.5	18.0	36.0
10	7.2	69.5	14.8	13.0	31.5	31.5	13.8	38.0
Mean	11.1	57.3	14.6	10.9	62.7	51.1	13.7	43.4

F = Forward rotation
B = Backward rotation

Comparison of the time constant of decay (π/Δ sec) [65] and initial slow phase velocity (ω_{to} °/sec) of nystagmus following rotation in pitch about vertical and horizontal axes, and in yaw about the vertical axis. Except where indicated, each value is the mean for rotation in the two directions.

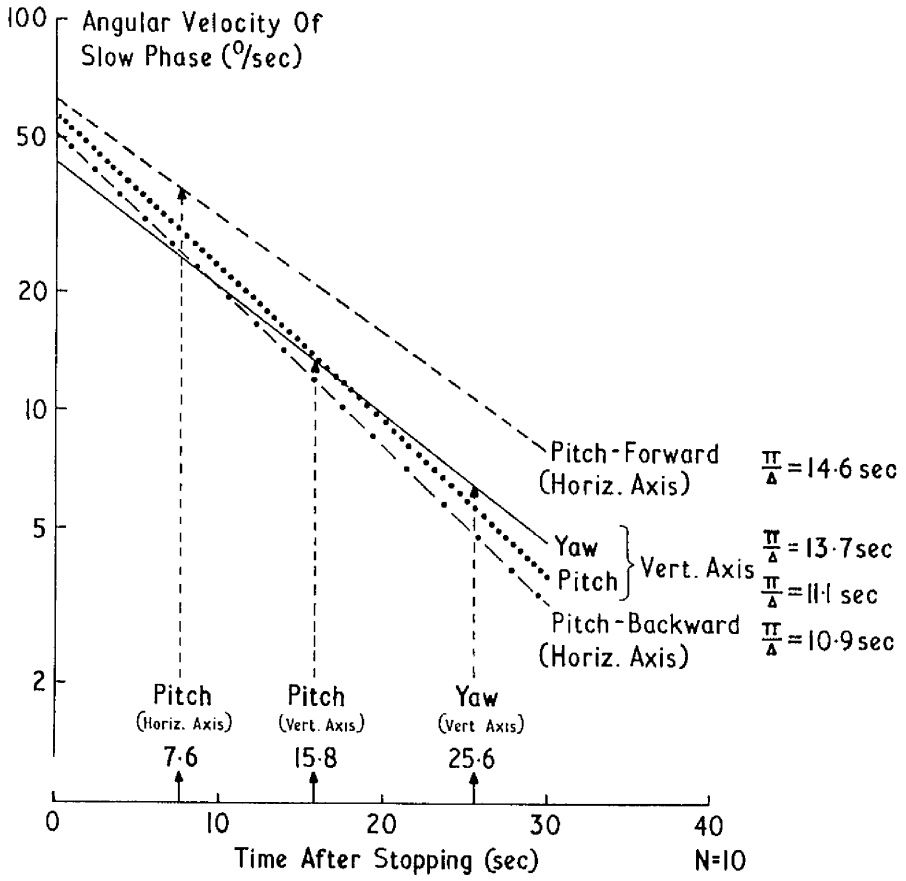


Figure 5.7

Comparison of the mean pattern of decay and nystagmus time constant (π/Δ sec), following impulsive deceleration from 60°/sec, in the different experimental situations. Based on results from 10 subjects. Velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale. Corresponding mean durations of after-sensations (sec) are indicated by arrows on the abscissa.

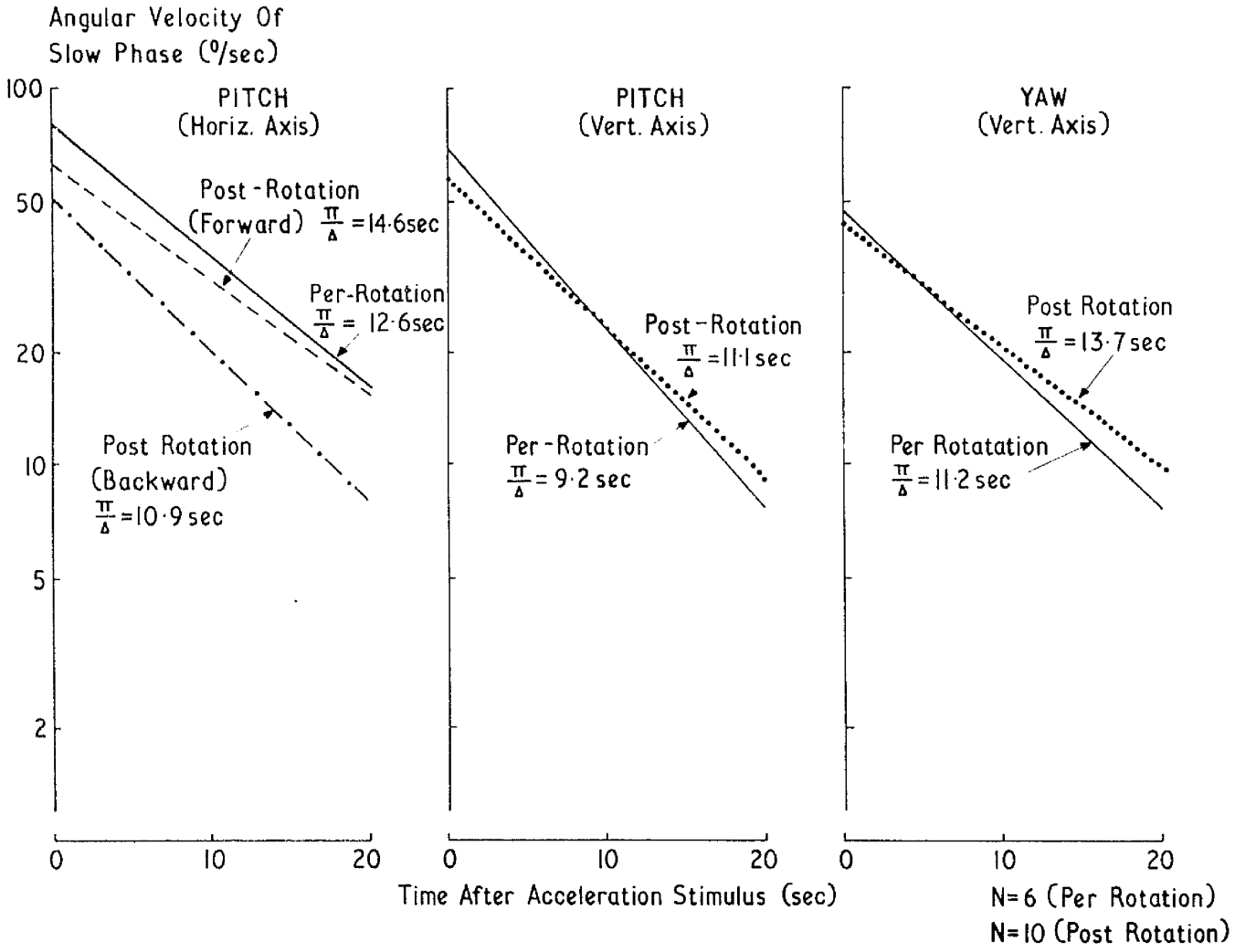


Figure 5.8

Comparison of the mean patterns of decay and time constants (π/Δ sec) of per-rotational nystagmus (6 subjects) and post-rotational nystagmus (10 subjects) in the different experimental situations. Slow phase velocity of nystagmus is plotted on a logarithmic ordinate scale.

according to the axis of rotation and the position of the subject. For rotation in pitch, the average 'threshold' was appreciably higher when the axis of rotation was horizontal (31.0°/sec) than when it was vertical (13.5°/sec), while the 'threshold' in yaw when the rotation axis was vertical (6.4°/sec) was much lower than either of those obtained in pitch.

The pattern of post-rotational nystagmus in the three experimental situations (Fig 5.7) was also compared with the pattern of decay of the per-rotational nystagmus obtained during the first three cycles of continuous rotation in these situations (Part 4, Section.2, Fig 4.27). For convenience, the data from these two figures has been plotted together in Fig 5.8. There was no significant difference between the per and post-rotational nystagmus time constants in any of these situations.

SUMMARY

Following rotation in pitch about horizontal and vertical axes, there was no appreciable difference either between the time constant of decay or the initial angular velocity of post-rotational nystagmus in the two axes. When the axis of rotation was horizontal, however, the nystagmus time constant was significantly greater following rotation in the forward than

the backward direction. The time constants of post-rotational nystagmus did not differ significantly from those of the comparable per-rotational nystagmus (Part 4, Section 2).

The duration of after-sensations in pitch was significantly shorter when the rotation axis was horizontal than when it was vertical, and this difference was found to be associated with an apparent elevation of the sensory 'threshold' when the axis of rotation was horizontal.

As with the experiment in the previous section, these findings might be explained either in terms of peripheral ('g on canal') or central ('somaesthetic inhibition') processes (Part 1 (2)). However, the differences in duration of after-sensations without corresponding changes in the nystagmus time constants of decay, as well as the apparent alterations in sensory 'threshold', favour an explanation of the present findings in terms of a central rather than a peripheral mechanism.

The results will be discussed more fully in Part 6.

PART 5

Section 3

The Effect of the Direction of the Gravitational Vertical on Post-Rotational Responses in Three Orthogonal Axes (Yaw, Pitch and Roll)

SECTION 3

COMPARISON OF THE EFFECT OF DIRECTION OF THE GRAVITATIONAL VECTOR ON POST-ROTATIONAL RESPONSES IN THREE ORTHOGONAL AXES (YAW, PITCH AND ROLL)

Purpose of Experiment

The experiments so far described have shown that vestibular responses, following angular acceleration stimuli in yaw or pitch, can be modified by the orientation of the subject to the gravitational vector.

In comparison with post-rotational responses about a vertical axis, however, when the rotation axis was horizontal, stimuli in yaw (lateral canals) reduced both sensations and the nystagmus time constant. Stimuli in pitch (vertical canals) reduced only the after-sensations, without producing an appreciable change in the pattern of decay of nystagmus. In contrast, a recent study (Melvill Jones, Barry and Kowalsky, 1964) showed a significantly greater time constant for post-rotational nystagmus in yaw than in either pitch or roll, although in these experiments the axis of rotation was always vertical, so that differences in the pattern of decay of nystagmus might have been due to factors associated with orientation to the gravitational vertical, rather than to intrinsic differences in the canal dynamics.

In an attempt to clarify these differing observations, a further comparative examination of vestibular responses in yaw, pitch and roll was carried out.

The experiment was performed, using a multi-position chair mounted on a turntable, to investigate changes in post-rotational responses to angular stimuli in each of the orthogonal body axes, produced when the orientation of the head and body to the gravitational vertical was altered. This was achieved by tilting the subject through 90° from the plane of rotation as soon as rotation of the turntable had stopped. The axes and planes of rotation, and repositioning manoeuvres used in this experiment, are illustrated diagramatically in the top half of Fig 3.6 (Part 3). The important feature in these procedures was that the 90° movement of the subject did not take place until after the (angular) stopping stimulus (i.e. when the subject was stationary), occupied only 2-3 sec, and was always in a plane perpendicular to that of the preceding rotation. Thus the repositioning manoeuvres, although stimulating otoliths and other gravi-receptor organs, did not provide an appreciable stimulus to the canals responding to the angular deceleration.

Particular attention was paid to the nature of subjective (illusory) after-sensations in the various experimental procedures, because it is these which conflict with other veridical cues, and in the flight environment may engender uncertainty about the position, motion or attitude of the aircraft (a potentially dangerous condition known as spatial disorientation).

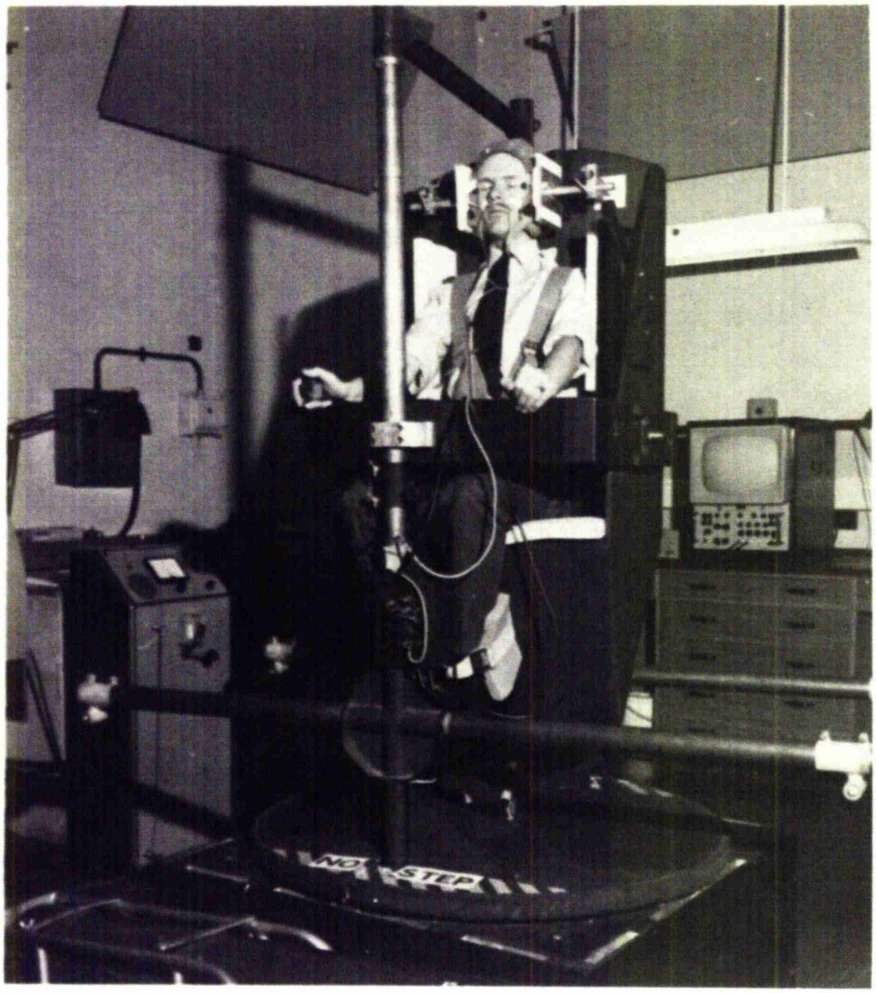


Figure 5.9

Variable-position chair and turntable assembly, with chair mounted for movement in the coronal plane. See also Fig 5.11.

METHOD

Apparatus

The experiment was carried out with the subject seated in a rectangular wooden chair, supported in a vertical tubular structure mounted on the turntable already described in Part 3 (2) (Figs 5.9 and 5.10). The chair was bolted to a square wooden frame which was fitted with two pairs of orthogonal trunnions, the axes of which passed close to the centre of gravity of the average subject. Either pair of trunnions could be fitted into open bearings attached to the vertical supports, so that the chair could be tilted through $\pm 90^{\circ}$ from the vertical in either the sagittal or coronal plane. Thus the subject could be reorientated either in pitch (y body axis) or roll (x body axis) according to the position in which the chair was placed in the vertical frame (Figs 5.9, 5.10 and 5.11).

The whole assembly could be smoothly rotated in either direction about a vertical axis by the servo-controlled electric drive to the turntable.

A standard aircrew harness, with additional downward straps between the legs, thigh straps, and adjustable metal side plates which supported the shoulders, provided adequate restraint for the subject in all chair positions. The head was immobilised by lateral plates and a broad canvas band over the forehead.

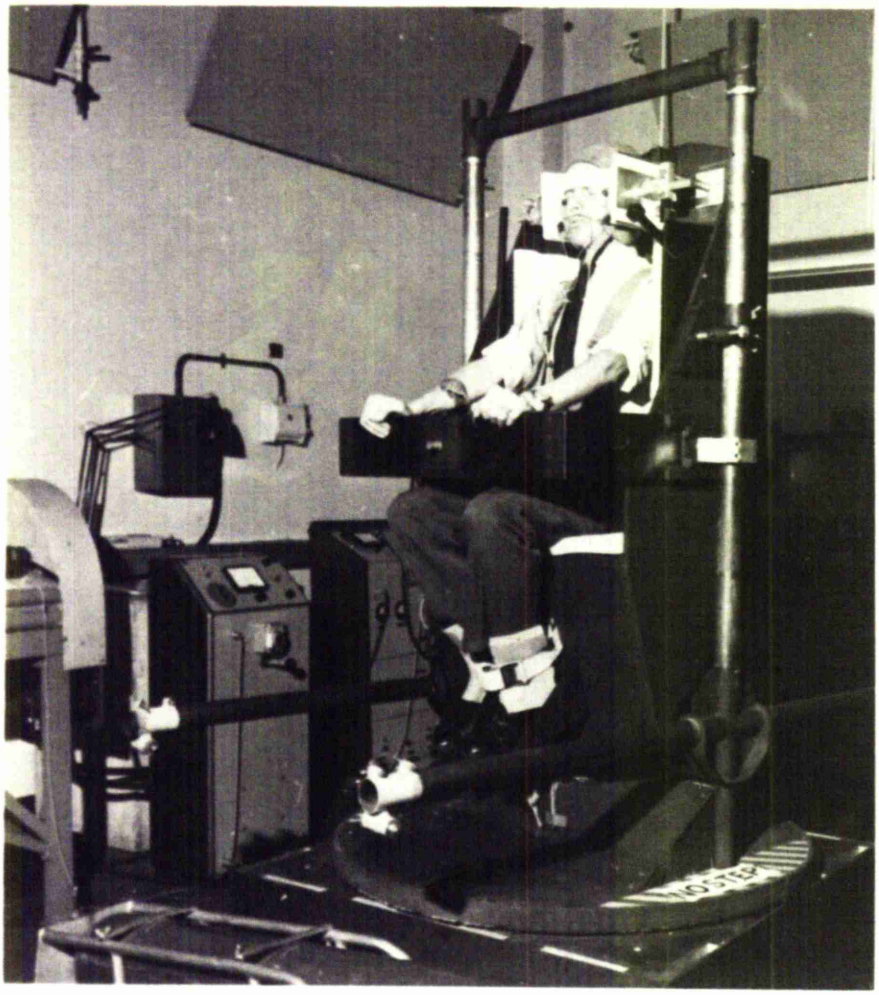


Figure 5.10

Variable-position chair and turntable assembly, showing the chair mounted for movement in the sagittal plane. See also Fig 5.11.

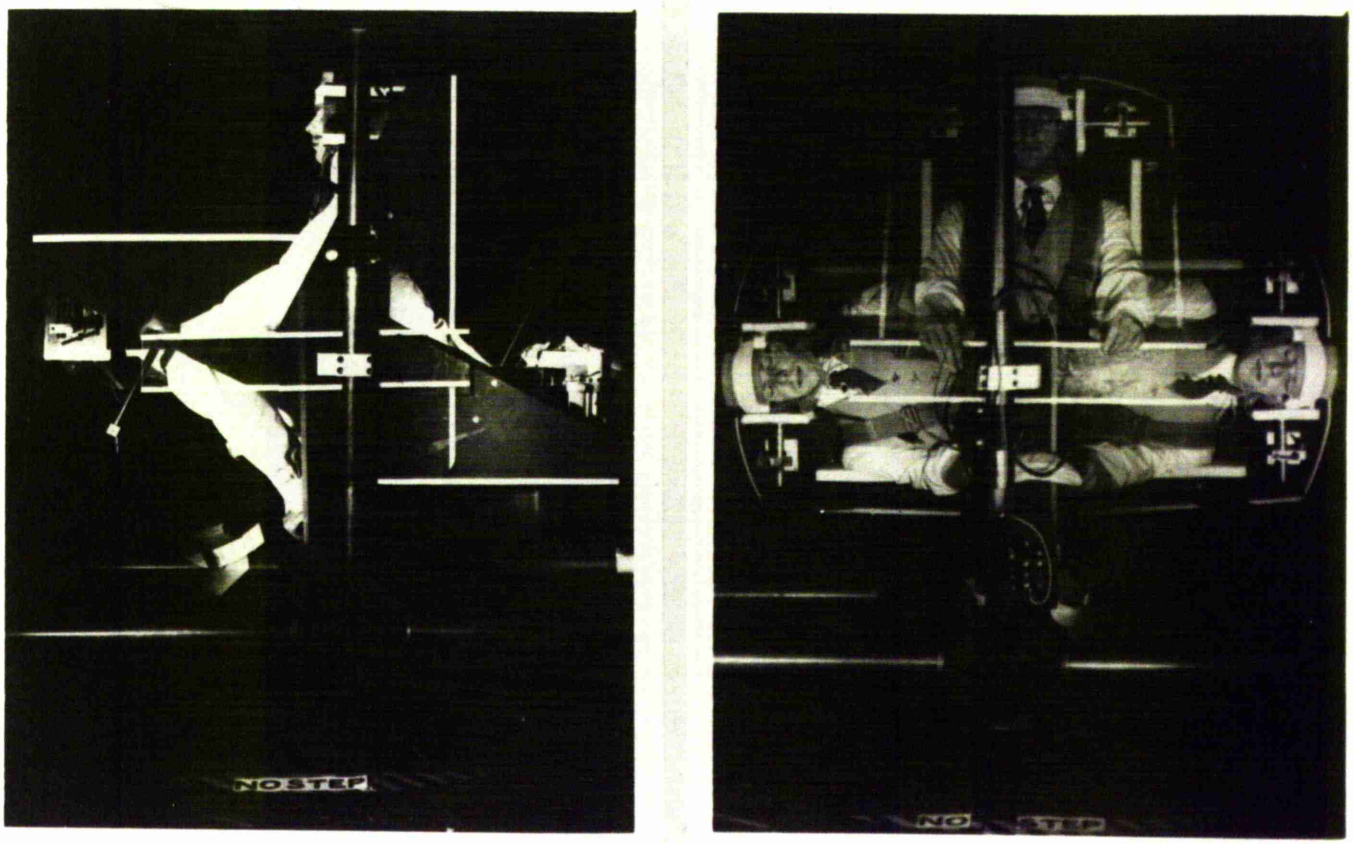


Figure 5.11

Variable-position chair and turntable assembly, showing range of angular movement in the sagittal and coronal planes, and the six positions used during the experiment.

Lateral (horizontal), or vertical, post-rotational eye-movements were recorded for 40 sec with the eyes closed, by DC electroculography (Part 3 (3/5)). Calibration eye-movements were made between successive runs, using a pair of small lights placed in front of the seated subject at the level of the head.

Conduct of experiment

Eight laboratory personnel (5 male, 3 female) acted as subjects. After the nature of the procedures to be carried out had been explained, the electrodes were applied, the subject strapped in position with the chair vertical, and a signalling key placed in their hand. Calibration eye-movements were recorded. The general procedure thereafter was as follows: The chair was positioned appropriately (as described below), and the subject instructed to relax with their eyes closed. They were also asked to concentrate on their after-sensations when rotation stopped, to press the key once each time they felt that they had moved through 90°, and to give several rapid presses when all sensation of turning finally disappeared. Apart from denoting the 'end point', these instructions were included in order to maintain the 'arousal level' of the subject.

The turntable was accelerated at $1°/sec^2$ to $60°/sec^2$, and this velocity was maintained for 60 sec before rotation was stopped. As soon as the turntable was stationary the

chair was tilted by hand through 90°. This procedure occupied only 2-3 sec, and was indicated by an event-marker on the galvanometer trace.

The experiment was divided into four parts, determined by the four reorientation procedures to be carried out. These were:

1. Yaw axis. The subjects were rotated in yaw seated upright in the chair. On stopping they were tilted in the sagittal plane to either the prone or the supine position (Fig 5.10 and 5.11).
2. Yaw axis. Rotation was as described in (1), but on stopping the subjects were moved in the coronal plane, to either a left-side-down or right-side-down position (Figs 5.9 and 5.11). In sessions 1 and 2, each of which comprised 6 runs, lateral (horizontal) eye-movements were recorded.
3. Pitch axis. The subjects were rotated lying either on their left or right side, and on stopping were tilted to the vertical position (Figs 5.9 and 5.11). Vertical eye-movements were recorded.
4. Rolling axis. The subjects were rotated lying either in the prone or supine position, and on stopping were moved to the vertical position (Figs 5.10 and 5.11). No eye-movements were recorded during this procedure. There were 8 runs in sessions 3 and 4.

Every procedure was carried out with rotation both in the clockwise and counterclockwise directions, and each subject experienced a total of 28 runs throughout the experiment. These included appropriate control runs in which, after stopping, the subject was not moved but remained in the plane of rotation. The sequence of runs within sessions was presented in a randomised order, and on completion of each session the subjects were asked to describe carefully the sensations aroused by the various procedures.

In two subjects a series of 'static' repositioning manoeuvres (i.e. without preceding rotation) were also performed, to investigate the effect of the angular stimuli associated with these procedures on the semicircular canals. 90^{o} movements were made, both in the sagittal and coronal planes, while lateral and vertical eye-movements were recorded.

RESULTS

Subjective Experiences

It is convenient to consider each axis of rotation separately, but only the main findings are included here. A more detailed description of subjective results, and particularly the alterations in the nature of after-sensations

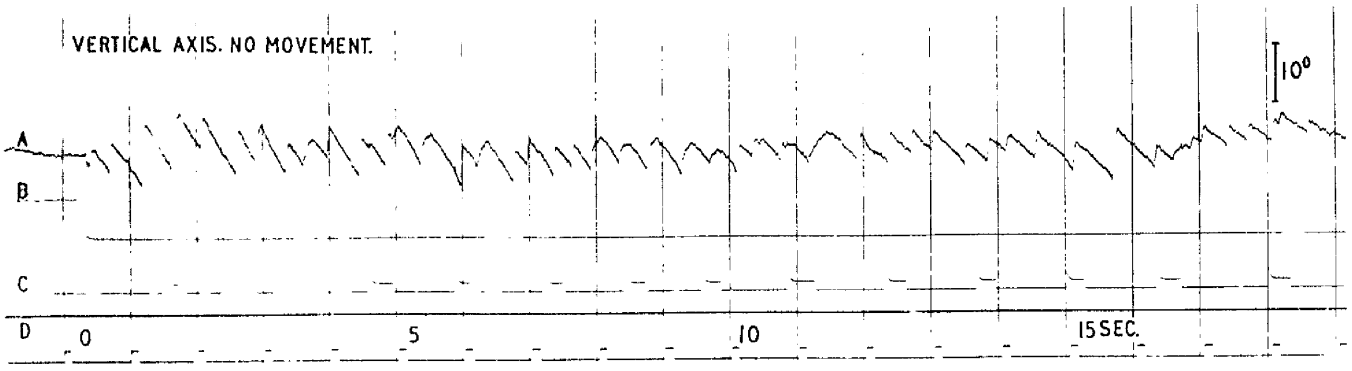


Figure 5.12

Record of lateral nystagmus (A) on stopping from rotation about a vertical axis (z body axis) at 60°/sec to the right (B). Subject responses (C) indicate successive (illusory) displacements of 90°.

in the three axes of rotation, when the subjects were repositioned, can be found in reference

Yaw Axis. The majority of subjects found difficulty in correlating their illusory sensations of turning with actual angular displacement, and most of the records contained only an indication of when the after-sensations finally disappeared. However, two subjects were able to make this assessment during their control runs, and to signal each time they felt that they had turned through 90°. The record from one of these subjects is shown in Fig 5.12, in which the progressive increase in the interval between responses demonstrates the exponential decay of the sensations engendered by the vestibular signal (Van Egmond, Groen and Jonkees, 1948).

The average duration of after-sensations in each position is shown in Table 5.6.

TABLE 5.6

Position of Subject	Duration of After-sensation (sec)
Vertical (control runs)	26.5
Moved to Prone	8.0
" " Supine	9.4
" " Right-side-down	8.6
" " Left-side-down	8.8

MEAN DURATION OF AFTER-SENSATIONS IN DIFFERENT POSITIONS (YAW AXIS)

The reduction in sensation times when the subjects were moved to the various horizontal positions was highly significant ($p = 0.001$), but there was no significant difference between the duration of sensations in the four horizontal positions.

These results agree with the general findings in Part 5, Section 1. They also accord with reports made by the subjects at the end of their test session, for without exception the strong after-sensations of rotation in yaw experienced in control runs were stated to be abolished "very quickly" as soon as movement to a horizontal position occurred.

Four subjects experienced mild nausea towards the end of their session, but this was transient and did not affect the conduct of the experiment.

Pitch Axis. Table 5.7 shows the mean duration of after-sensations in the different situations.

TABLE 5.7

Position of Subject	Duration of After-sensation (sec)
Right-side-down (R.S.D.)	11.9
Left-side-down (L.S.D.)	12.2
R.S.D. Moved to Vertical	9.2
L.S.D. Moved to Vertical	9.8

MEAN DURATION OF AFTER-SENSATIONS IN DIFFERENT POSITIONS (PITCH AXIS)

The duration of after-sensations following movement to the vertical position was significantly shorter ($p = 0.01$) than when the subjects remained in the horizontal plane, though the magnitude of this reduction was very much less than when the subjects were repositioned following angular stimuli in yaw (Table 5.6). There was no significant difference between the sensations in the left and right-side-down positions.

In the control runs, in which subjects remained in the plane of rotation, the after-sensations were of the expected form - namely a feeling of pitching head over heels in the horizontal plane, either forwards or backwards, in a direction opposite to that of the preceding rotation.

The nature of these sensations was appreciably altered, however, when the subjects were moved to the vertical. Most of them reported an immediate intensification of their sensations during the period in which they were repositioned, although thereafter the sensations seemed to pass off more quickly than when they were not moved. In addition, each subject noted a concomitant change in the plane of the sensed rotation as they were brought to the vertical. Most of them stated that the plane of rotation seemed to move with the tilt through approximately 90°, so that their initial sensation of pitching in the horizontal plane was transferred to one of movement in a vertical sagittal plane. The majority of subjects also noticed a change in the character of their sensations, and that on assuming

the vertical position they no longer experienced a true sense of rotation, but more a feeling of "moving without getting anywhere", or of "displacement" rather than motion.

The tilting procedures in this part of the experiment were rather unpleasant, and the majority of subjects were nauseated, some quite severely, by the end of their session.

Rolling Axis. The findings here were essentially similar to those for the pitch axis. The mean duration of after-sensations shown in Table 5.8, was shorter ($p = 0.05$) when the subjects were moved to the vertical position than when they remained horizontal, though the magnitude of the reduction was less than that observed in the yaw or the pitch axes.

TABLE 5.8

Position of Subject	Duration of After-sensation (sec)
Prone) (Control runs)	17.8
Supine)	13.4
Prone Moved to Vertical	12.8
Supine Moved to Vertical	11.8

MEAN DURATION OF AFTER-SENSATIONS IN DIFFERENT POSITIONS (ROLLING AXIS)

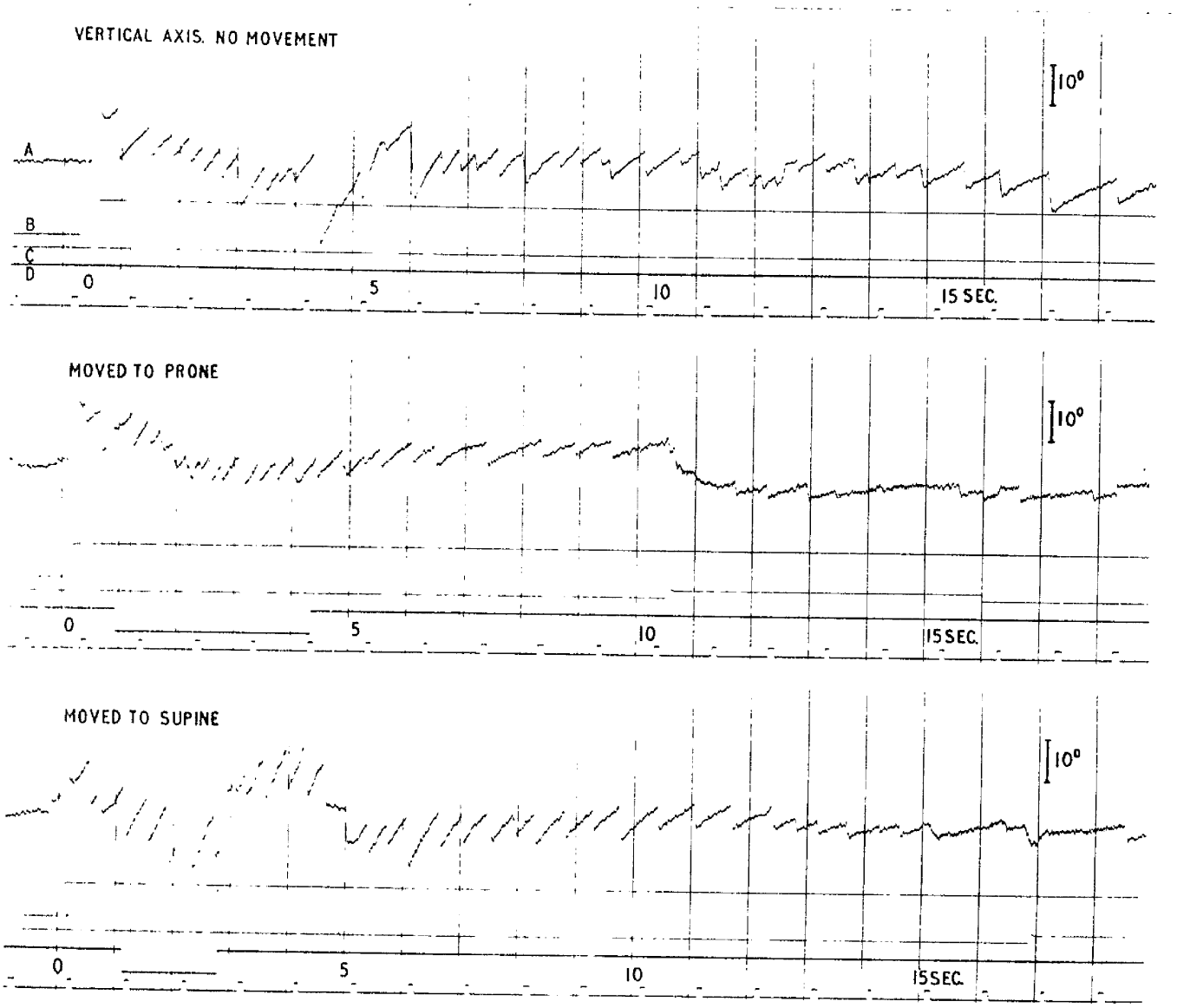


Figure 5.13

Record of lateral nystagmus (A) on stopping from rotation in yaw about a vertical axis (z body axis) at 60°/sec to the right (B). In the middle and lower records the subject was moved in the sagittal plane from vertical to the prone or supine position respectively, during the time indicated by trace D. Termination of after-sensations, following movement to horizontal positions, is shown on trace C.

In addition, in control runs when the subjects remained horizontal after stopping, the sensations were significantly longer ($p = 0.05$) in the prone than in the supine position (Table 5.8), though there was no effect attributable to position in the reduction of after-sensations when subjects were moved from the horizontal to vertical.

The descriptions of after-sensations experienced in control runs, and when the subjects were repositioned to vertical, were also similar to those already described for the pitch axis, with the substitution of 'rolling' for 'pitching' and 'coronal' for the 'sagittal' plane. However, the incidence of nausea was higher in this part of the experiment, for all of the subjects were nauseated at the end of their test schedule. The majority of subjects also stated that reorientation following rolling axis stimulation was "more unpleasant" than when the stimulus was applied in pitch.

Post-rotational Nystagmus

Yaw Axis. Lateral (horizontal) eye-movements were recorded for 40 sec after rotation was stopped. Figs 5.13 and 5.14 show a typical series of recordings from two subjects, following rotation in yaw. The top record in each figure is the control, in which the subject remained vertical throughout. The traces below show the pattern of nystagmus when they were tilted through 90°, as soon as rotation was stopped, to the horizontal positions indicated. From

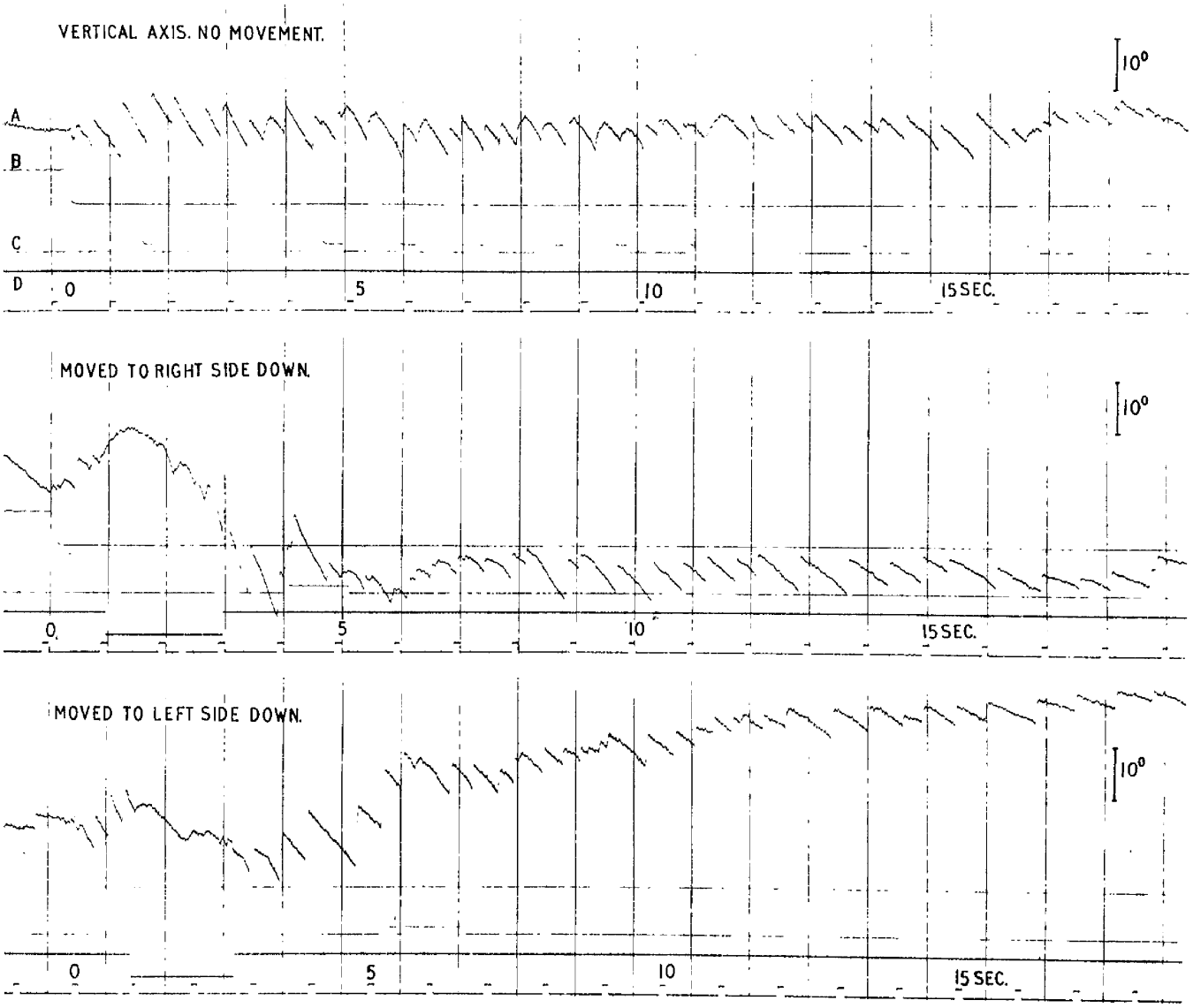


Figure 5.14

Effect of reorientation in the coronal plane, from vertical to the horizontal (right or left-side-down position), on lateral nystagmus following rotation in yaw about a vertical axis at 60°/sec to the left. Other details as in Figure 4.13.

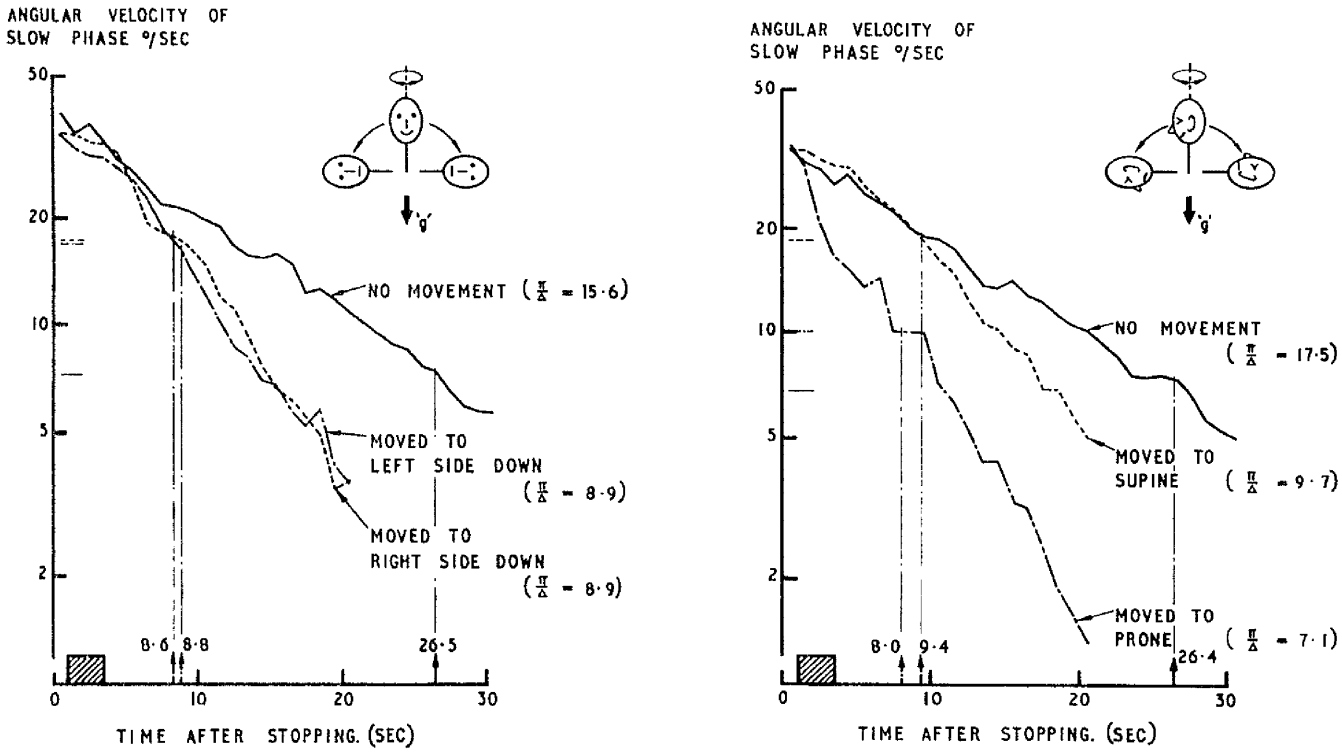


Figure 5.15

Mean pattern of decay and time constant of nystagmus (π/Δ sec), following impulsive deceleration from 60°/sec about a vertical axis, with the subject in different positions. Based on results from 8 subjects. The corresponding durations of after-sensations (sec) are indicated by arrows on the abscissa. Angular velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale. The shaded block shows the period during which subjects were repositioned.

inspection of these records it can be seen that the nystagmus decayed appreciably more quickly when the subjects were horizontal than when they remained vertical. Comparison of the amplitude and frequency of eye-movements in the prone and supine positions (Fig 5.13) also shows that the rate of decay of nystagmus was more rapid in the former than in the latter position. There was no apparent disparity in the rate of decay of nystagmus in the left and right-side-down positions, however (Fig 5.14).

The eye-movement records were analysed quantitatively (Appendix 1A), and a graphical representation of the mean pattern of post-rotational nystagmus in the different experimental situations (Fig 5.15) obtained in the manner previously described (Part 5, Section 1).

From the individual log-linear plots for each subject, the time constant of decay (π/Δ) and initial slow phase velocity (ω_{to}) were determined (Appendix 1B). Statistical analysis of these values, by the methods already described (Part 3 (B)), showed that the time constants changed with the orientation of the subject in a similar manner to the after-sensations (Table 5.6). Thus the decay of nystagmus was significantly slower ($p= 0.01$) when the subjects remained vertical (π/Δ 15.5 sec) than when they were moved to the various horizontal positions. The rate of decay when the subjects were prone (π/Δ 7.1 sec) was also significantly more

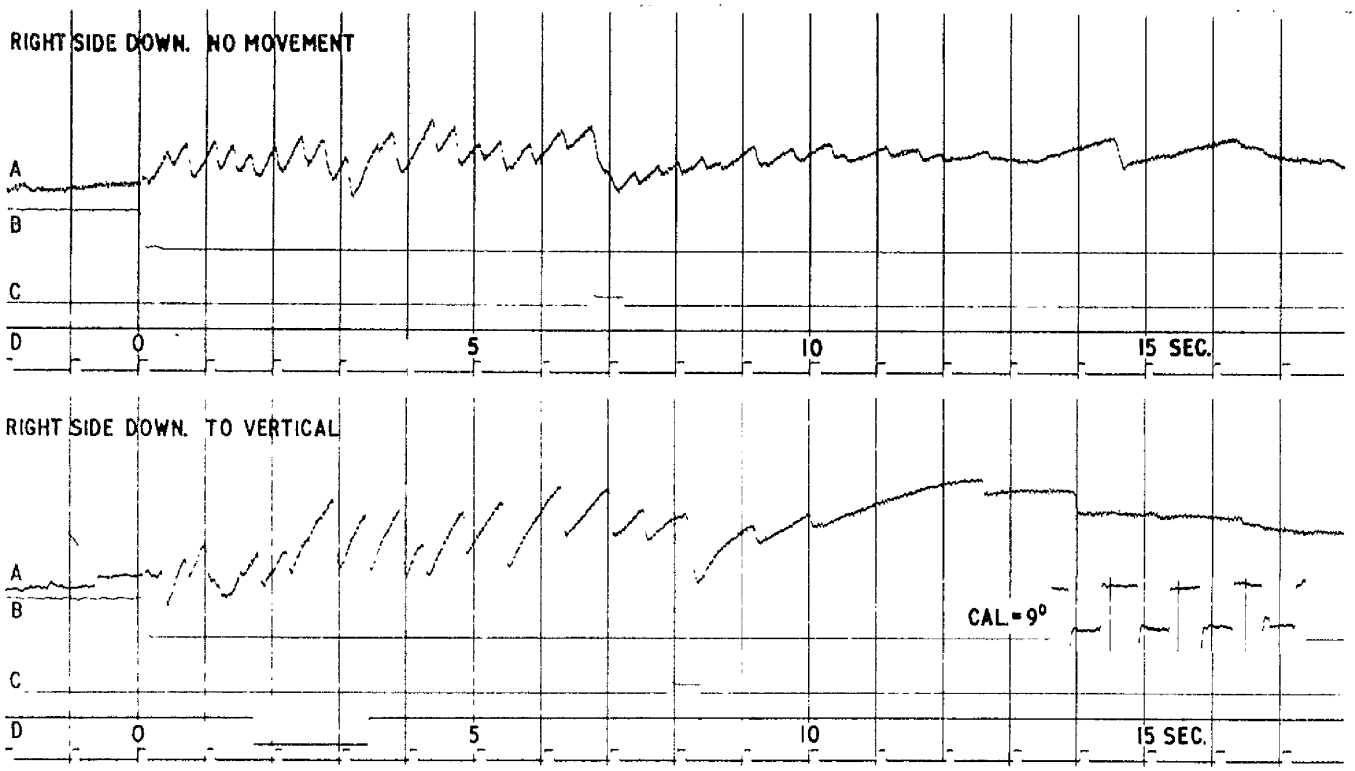


Figure 5.16

Record of vertical nystagmus (A) on stopping from rotation in pitch about a vertical axis (y body axis) at 60°/sec to the left. In the lower record, reorientation of the subject from horizontal (right-side-down position) to the vertical occurred during the time indicated on trace D.

rapid (p= 0.01) than when they were supine (π/Δ 9.7 sec), but there was no difference between the time constants in the left or right-side-down positions (π/Δ 8.9 sec).

Pitch Axis. Vertical eye-movements were recorded for a period of 30 sec after rotation was stopped. Only six of the subjects produced adequate post-rotational nystagmus, and in the majority of these the general quality of response was inferior to that on the lateral eye-movement records. Fig 5.16 shows the records of vertical nystagmus obtained from one of the subjects in two situations. There was no obvious change in the pattern of vertical nystagmus when the subjects were repositioned in the post-rotation period.

The eye-movement records from the six subjects who produced measurable vertical nystagmus were analysed in the same manner as the horizontal nystagmus, and the mean decay curves for the various experimental situations determined (Fig 5.17). For the individual subjects, the time constant of decay in each of the experimental conditions was obtained from the slope of the calculated regression equation. Analysis of variance of these values showed that the time constant was somewhat smaller (p= 0.05) when the subjects were moved to the vertical position (π/Δ 5.9 sec) than when they remained horizontal (π/Δ 7.5 sec). There was no significant difference between time constants in the right and left-side-down positions.

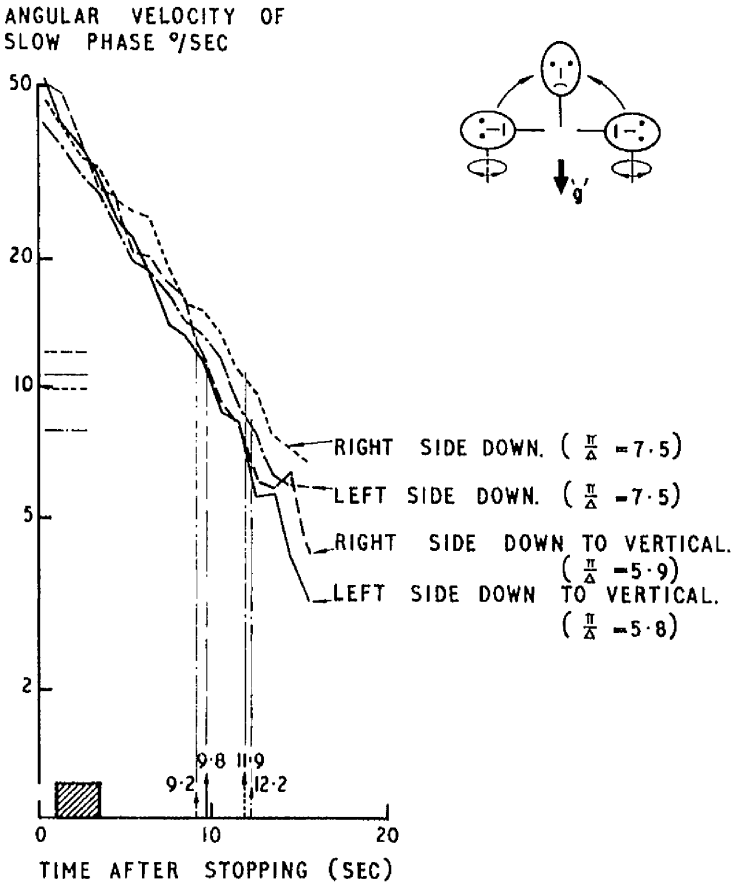


Figure 5.17

Mean pattern of decay and time constant of vertical nystagmus (π/Δ sec), following impulsive deceleration from 60°/sec in pitch about a vertical axis (y body axis). Based on results from 6 subjects. Other details as in Fig 5.15.

Changes of Sensory 'Threshold' in Yaw and Pitch

In Figs 5.15 and 5.17 the average sensory 'thresholds' have been delineated in the manner previously described (Part 5, Section 1), i.e. as the slow phase nystagmus velocity corresponding to the time at which after-sensations passed off. In yaw, (Fig 5.15), when the subjects were vertical, after-sensations persisted until the nystagmus slow phase velocity had fallen to 7.0°/sec, while the corresponding 'threshold' values after movement to the horizontal plane were equivalent to nystagmus velocities of only 10.0°/sec (prone), 18.5°/sec (supine) and 17.0°/sec in the left and right-side-down positions respectively. Following rotation in pitch (Fig 5.17) the 'threshold' changed from an average value of 9.0°/sec when the subject remained in the horizontal plane (right or left-side-down), to an average of 11.0°/sec when they were moved to the vertical. These findings imply that following stimuli in yaw and pitch, the sensory 'threshold' was raised when the subjects were re-positioned after rotation was stopped.

Eye-movements During 'Static' Repositioning Manoeuvres

Two subjects were repositioned through 90°, both in the sagittal and coronal planes, without preceding rotation. The records of lateral and vertical eye-movements obtained during these procedures showed no evidence either of nystagmus, or of appreciable eye-deviation from the resting position.

SUMMARY

Sensations and nystagmus evoked by impulsive deceleration in the yaw, pitch and roll axes, were compared when the subjects remained in the plane of rotation, and when they were tilted through 90° as soon as rotation had stopped.

Irrespective of the axis of rotation, reorientation of the subject produced a significant reduction in the magnitude of after-responses, though this was appreciably greater in yaw than in pitch or roll. In the yaw and pitch axes, the reduction in after-sensations was also greater than the decrement in the corresponding nystagmus time constants, and this difference was found to be associated with an apparent increase in sensory 'threshold' when the subjects were repositioned.

Where comparable, these findings are in general agreement with those of the experiments in the two previous sections. In common with these experiments, however, they do not provide adequate information to distinguish between the role of peripheral and central processes in the causation of the effects observed.

The results will be considered in detail in Part 6.

PART 5

Section 4

Further Investigation of the Effect of Changing Orientation to the Gravitational Vector on Post-Rotational Responses Following Stimuli in Yaw about a Vertical Axis

SECTION 4

FURTHER INVESTIGATION OF THE EFFECT OF CHANGING ORIENTATION TO THE GRAVITATIONAL VECTOR ON POST-ROTATIONAL RESPONSES FOLLOWING STIMULI IN YAW ABOUT A VERTICAL AXIS

Purpose of Experiment

The experiments described so far have been concerned only with the effects of 90° differences in alignment of the subject to the gravitational vertical. In these circumstances, in which responses from two extreme positions in the range of orientation to gravity were examined, it was shown that the magnitude of the reduction in after-responses was greater for angular stimuli in yaw (lateral canals) than in pitch and roll (vertical canals). It was also noted that these experiments did not provide information which would enable the relative importance of peripheral ('g on canal') as opposed to central ('somaesthetic inhibition') processes to be determined. Indeed the main findings in the earlier experiments might equally well be explained in terms of either mechanism.

To attempt to distinguish between these mechanisms, therefore, and try to clarify the processes primarily responsible for alterations in post-rotational responses related to the position or change in orientation of subjects

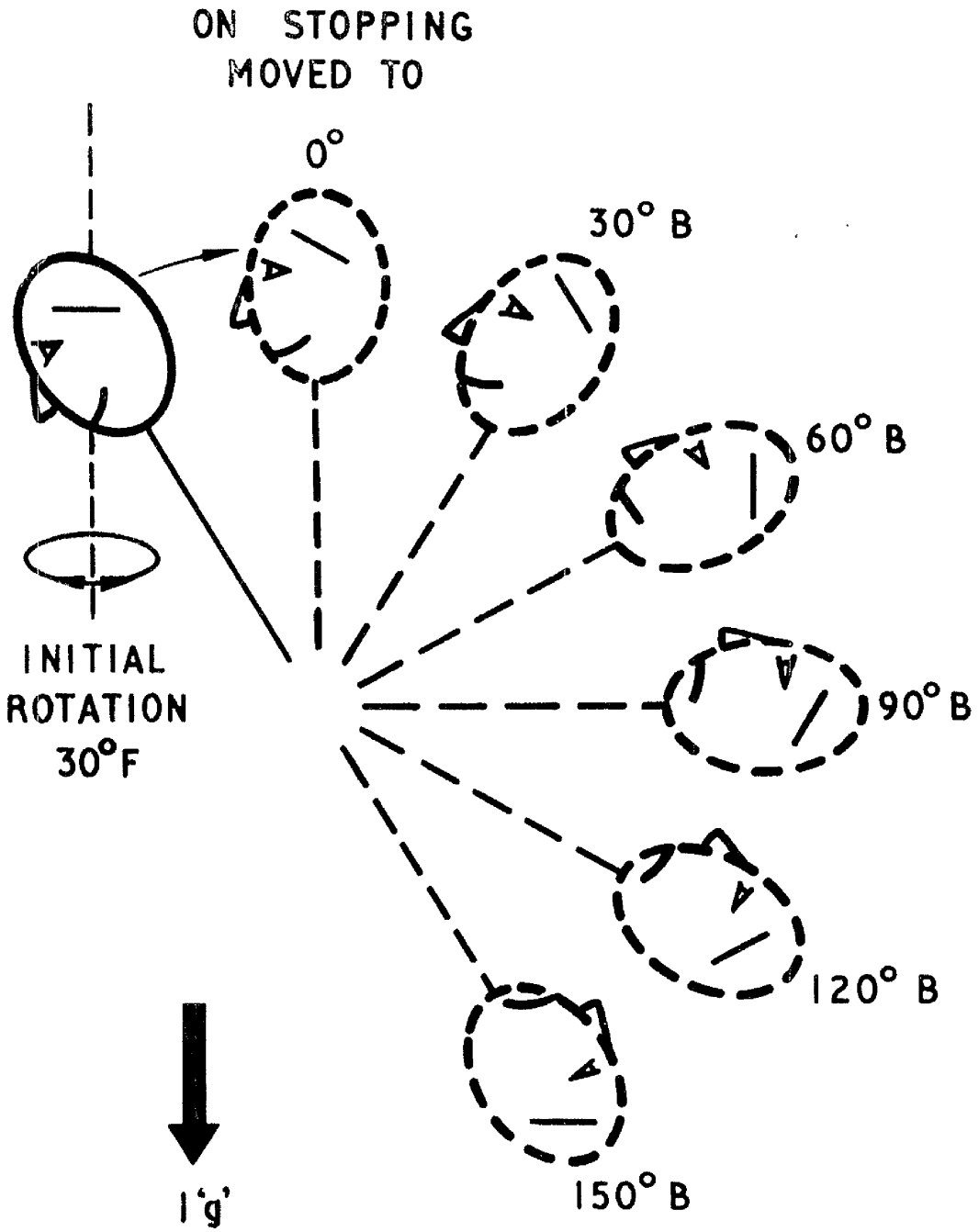


Figure 5.18

Diagram showing the positions in the sagittal (pitch) plane to which the chair could be moved, from 30° forward (F) to 150° back (B). The orientation of the lateral semicircular canals to the gravitational vertical is indicated by a short line in each diagram.

to the gravitational vertical, three further experiments were carried out. These investigated the behaviour of the lateral semicircular canals in greater detail.

The first experiment is described in the present section. Subjects were rotated in yaw about a vertical axis, and as soon as rotation was stopped repositioned in the sagittal plane. The general procedure was similar in principle to the first part of the last experiment. But in the present experiment, instead of a single 90° movement, the subjects were reorientated to seven different positions over an arc of 180° (Fig 5.18), so that post-rotational response in intermediate positions could be examined.

METHOD

Apparatus

The experiment was performed using the turntable and variable-position chair assembly described in the previous section (Fig 5.10). The chair was mounted so that it could be moved in the sagittal (pitch) plane to seven different positions from 30° forward to 150° back (Figs 5.18 and 5.19). Lateral (horizontal) post-rotational eye-movements were recorded for 30 sec with the eyes closed, by DC electro-culography (Part 3 (3)), and also calibration eye-movements between successive runs.

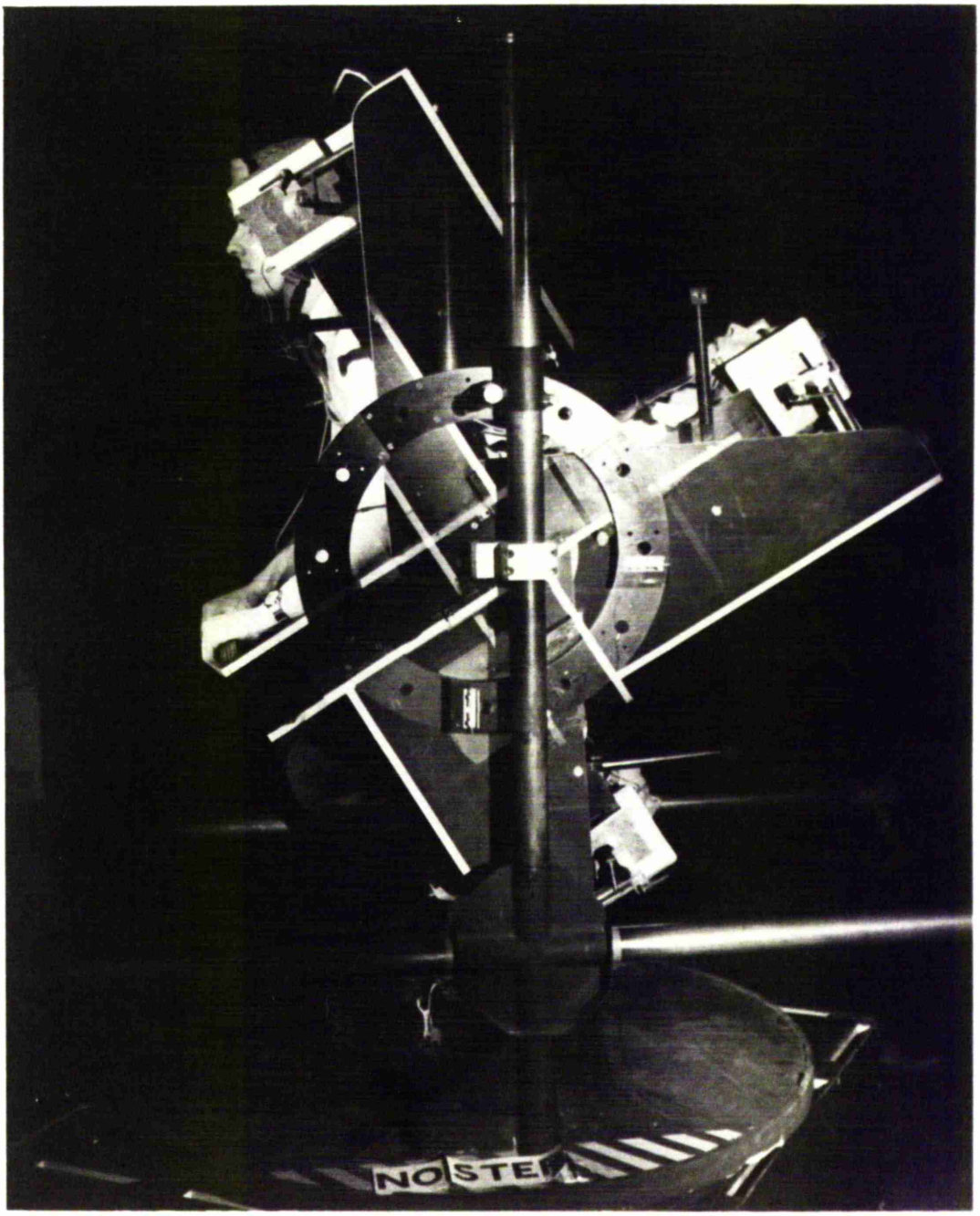


Figure 5.19

Turntable and variable-position chair assembly, showing some of the positions used in the experiment.

Conduct of Experiment

The experiment was carried out on two groups of ten male subjects (A & B). Each subject was rotated in yaw about a vertical axis, with the chair inclined 30° forward in pitch so that the plane of the lateral (horizontal) canals was normal to the gravitational vector (Fig 5.18). In all other respects the preliminary procedures and conduct of the experiment during rotation were the same as those described for rotation in yaw in the previous section.

When rotation was stopped, subjects in Group A were either not moved (remained 30° forward), or reorientated to the vertical (0°), 30°, 60° or 90° back positions. They were asked to concentrate on their after-sensations of turning and to indicate by pressing a key when these finally passed off. It was originally intended to limit the experiment to these five positions. In the light of the results obtained, however, for reasons which will be explained later, it was decided to extend the investigation to include reorientations up to 180°, and for this purpose a second group of subjects was used. Following the decelerative impulse, the subjects in Group B were reorientated to either 60°, 90°, 120° or 150° back positions (Figs 5.18 and 5.19). In addition, these subjects were instructed to ignore their after-sensations, and instead to perform mental arithmetic (as an 'arousal' task) during the post rotation period.

In both groups an attempt was made to 'standardize' somaesthetic cues engendered by the repositioning manoeuvres by swinging the subject through an arbitary arc of 120°, which occupied about 1-2 sec, during each reorientation procedure. Following reorientation, the subject remained in the new position, with eyes closed, until recording was discontinued after 30 sec.

Each subject experienced ten separate runs, which were carried out for rotation both to the left and the right, and presented in randomised order according to a Latin-square design. Appropriate control runs were also incorporated, in which the subjects were not moved in the post-rotational period.

RESULTS

Subjective Experiences

Only the subjects in Group A were asked to pay attention to after-sensations. The average duration of these sensations in each position, for the 10 subjects in this group, is shown in Table 5.9.

TABLE 5.9

Position of Subject	$30°_F$	0°	$30°_B$	$60°_B$	$90°_B$
Duration of after-sensations (sec)	15.3	16.3	12.3	12.9	12.9

MEAN DURATION OF AFTER-SENSATIONS IN DIFFERENT POSITIONS (Group A subjects)

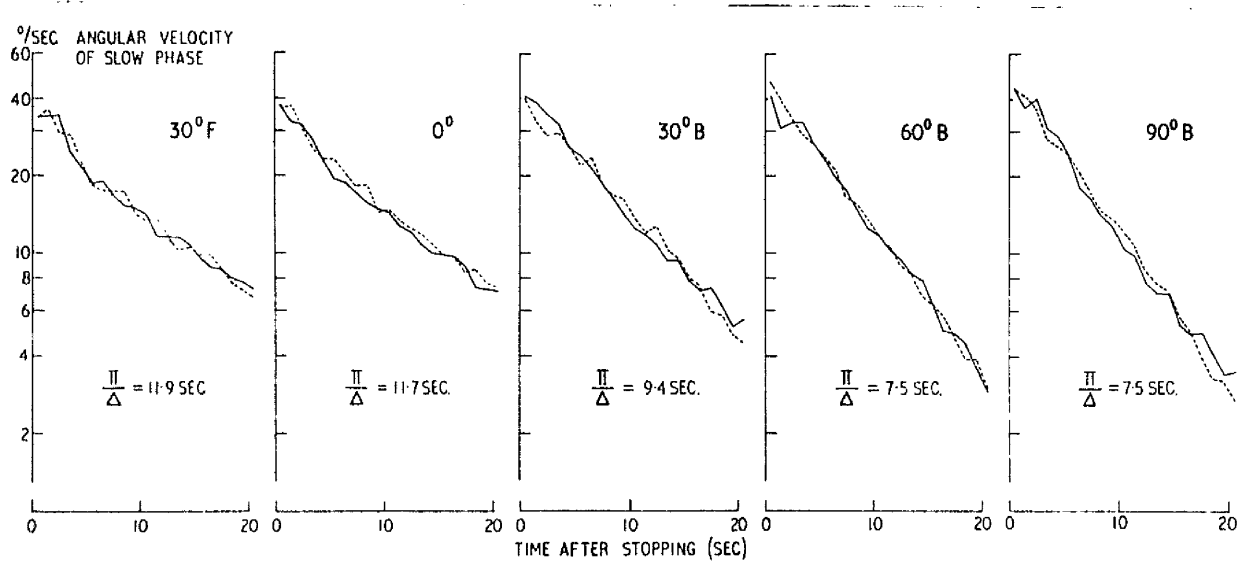


Figure 5.20

Comparison of the mean pattern of decay and time constant of nystagmus (π/Δ) for different orientations of subject to the gravitational vertical, following rotation in yaw at 60°/sec about a vertical axis. Based on results from the 10 subjects in Group A. Angular velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale.

These results, where comparable, are in general agreement with the findings of previous experiments (Part 5, Sections 1 & 3) in which, following stimuli in yaw, the duration of after-sensations was greater when the subjects remained vertical than when they were horizontal. However, in the present experiment the difference was much less than previously recorded, mainly because the after-sensations in the vertical position were shorter than in the previous experiments. This might perhaps be attributed to an inhibitory effect of somaesthetic signals engendered by the relatively larger (120°) movement which accompanied repositioning the subject, and would reduce the after-responses in the upright (0°) position, compared with those recorded when the subjects were vertical in the earlier experiments, in which no artificial movement was introduced following the stopping stimulus.

In the intermediate positions between 30° forward and 90° back, the mean duration of after-sensations did not show the progressive reduction, as might be expected on theoretical grounds, or conform with the measurements of time constants of post-rotational nystagmus in these positions (Fig 5.20). This was due largely to considerable scatter in the after-sensation measurements recorded in each position, and demonstrated that for small differences in orientation to the gravitational vertical, subjective responses are a relatively insensitive index of vestibular behaviour.

The descriptions of after-sensations obtained from the subjects in Group A were essentially similar to those described for stimuli in yaw in the previous section. In control runs, the after-sensations of turning were of the expected form, and generally stated to be in the horizontal plane. Following movement to positions intermediate between 30° forward and 60° back, most of the subjects felt that the plane of their sensations tilted backwards by an amount approximately equal to the angular difference between their initial and final positions. Thus in Fig 5.18, the short line which represents the lateral (horizontal) semicircular canal in each diagram, also indicates approximately the plane of after-sensations for the majority of subjects in these positions. The plane of after-sensations was thus apparently related to the alignment of the subject to the gravitational vertical, rather than to factors associated with the repositioning movements.

Changes in the intensity of after-sensations, and also the incidence of nausea, were similar to those described in the last experiment. Nausea appeared to be related to the number of impulsive stimuli received, as previously, and to some extent also to the nature of the repositioning movements. Seven subjects experienced mild nausea, though they were able to complete their test schedule, but three potential subjects had to be replaced because of severe nausea or vomiting during the experiment. Most of the incidents of nausea occurred towards

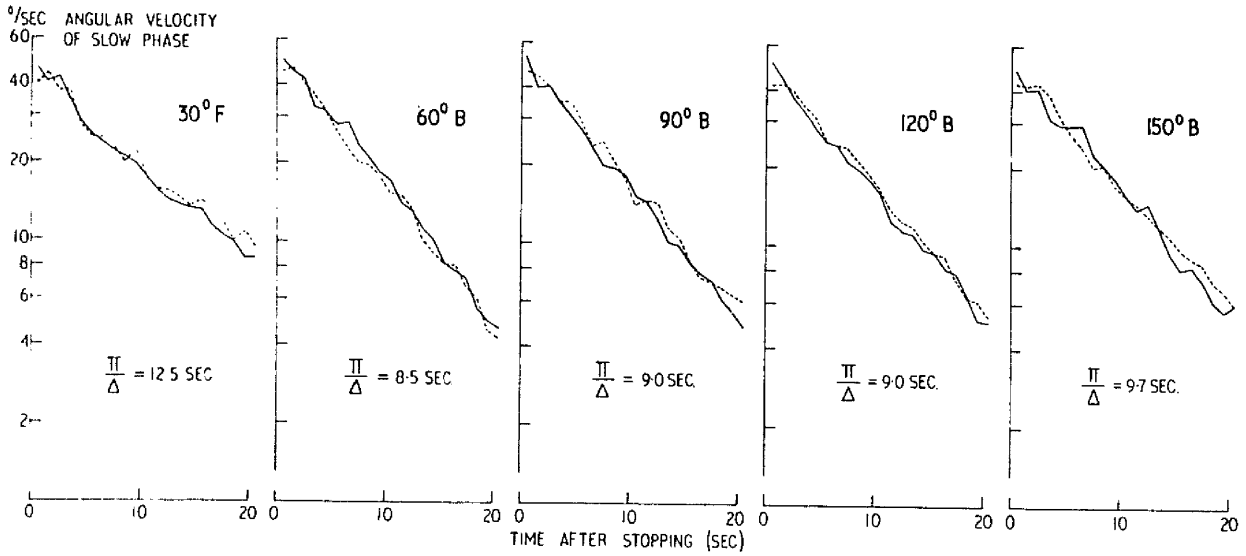


Figure 5.21

As Figure 5.20, for the 10 subjects in Group B.

the end of a session, but several subjects found repositioning to the vertical or 30° positions, in which a sharp oscillatory motion was necessary to accomplish the 120° swing, "particularly unpleasant".

Post-rotational Nystagmus

Quantitative analysis of the eye-movement records, and determination of the time constant of decay of nystagmus in each position, was carried out in the manner described in Appendix 1A & 1B. The average plots of log slow phase nystagmus against time after stopping, for the ten subjects in each group are shown in Figs 5.20 and 5.21. For the subjects in Group A (Fig 5.20), the rate of decay of post-rotational nystagmus was found to increase (time constant decrease) progressively as the angular reorientation of the subject to the gravitational vertical increased, from a maximum in the 30° forward position to minimum in the 60° back position. There was no significant difference between the time constant in the 30° forward and 0° positions, but the time constant in the 30° back position differed significantly both from these values ($p = 0.001$), and from the time constant in the 60° back position ($p = 0.05$). If these changes were related, in part, to the magnitude of the coplanar g-vector, then it might be expected that the rate of decay of nystagmus would decrease again (time constant increase) in a similar fashion for angular reorientations greater than 60°, with

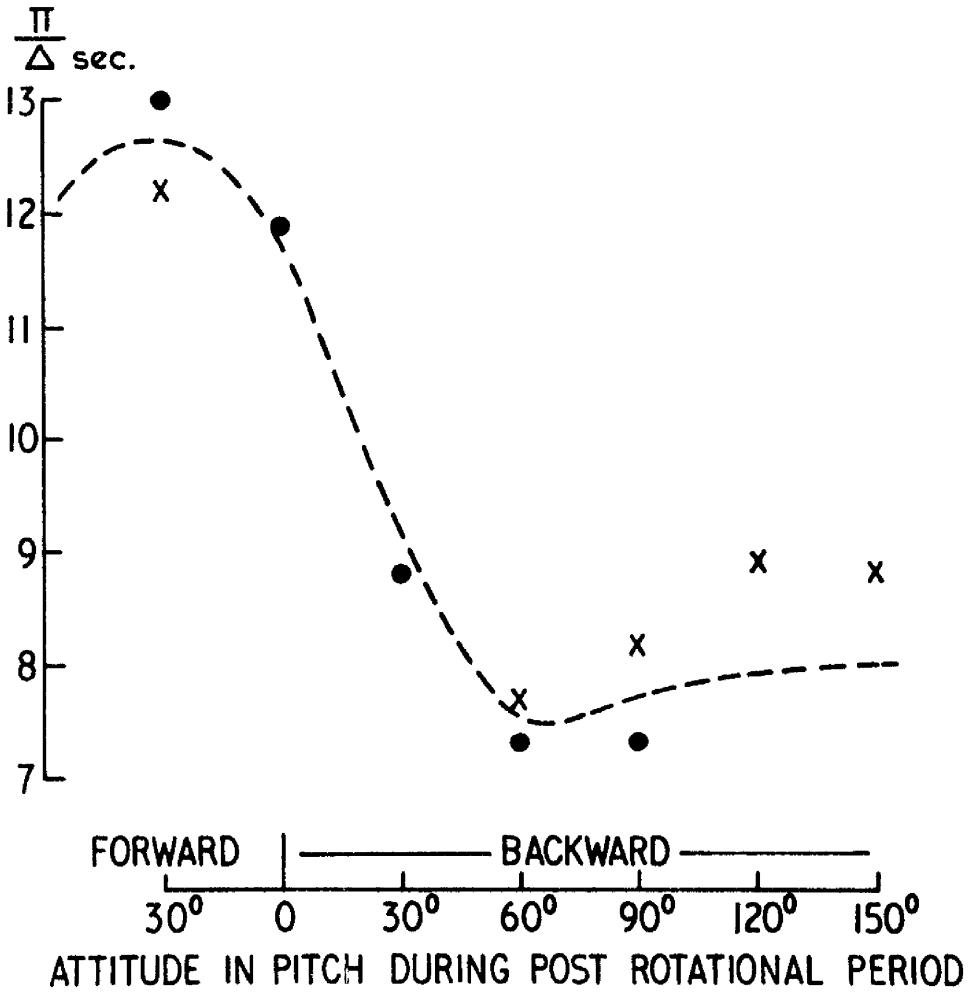


Figure 5.22

General relationship between nystagmus time constant of decay (π/Δ) and position of the subject in the post-rotation period. Based on mean results for the 10 subjects in Group A (●) and Group B (✖).

the time constant of decay in the 90° position similar to that in the 30° back position. But there was no evidence of such a change in the data from these subjects, and the time constants in the 60° and 90° back positions did not differ significantly from one another.

Clearly it was desirable to obtain further observations, and accordingly the experiment was extended, using the second group of subjects, to include reorientations up to 180° from the position occupied during rotation. Comparison of the average time constants in different positions for the subjects in Group B (Fig 5.21), showed a similar difference in the rate of decay of nystagmus between the 30° forward and 60° back positions ($p = 0.001$) to that observed in Group A subjects (above). But for reorientations greater than 90° there was only a slight increase in time constant, and no significant difference between the time constants in the 90°, 120° and 150° back positions.

Different subjects were used in Groups A and B, but the nystagmus time constants obtained in control runs, and following repositioning to the 60° and 90° back positions, did not differ significantly between the two groups. Accordingly the data from both groups was combined, to obtain the average curve shown in Fig 5.22, which depicts the general relationship between time constant of decay and post-rotational orientation of the subject to the gravitational vertical, over an arc of 180°.

SUMMARY

Following stimuli in yaw about a vertical axis, with the plane of the lateral canals normal to the gravitational vector, subjects were moved in the sagittal plane to 7 different positions over an arc of 180°. The nystagmus time constant was maximum in the initial (30°) forward position, decreased progressively as angular displacement from the vertical increased, to a minimum after a 90° change of alignment to the gravitational vector, but thereafter increased only slightly and remained practically constant for displacements between 90° and 180°.

Where comparable, these results agree with the findings of previous experiments (Part 5, Sections 1 & 3). They also demonstrate, for angular displacements up to 90° from the vertical, a close correlation between post-rotational orientation of the subject to gravity and the magnitude of reduction in the nystagmus time constant. This finding, in part, might be related to the magnitude of the coplanar component of g-vector. On theoretical grounds, however, irrespective of the precise nature of the underlying mechanism, it might have been expected that the overall relationship (i.e. including time constants in the quadrant 90°-180°, as depicted in Fig 5.22), would have shown a sinusoidal form. For example, in the 150° back position, the alignment of the body to the gravitational vertical was parallel to that in the

30° forward position, the gravitational vector was again normal to the stimulated (lateral) canals (Fig 5.18), while the plane of illusory sensations was horizontal and therefore not in conflict with somaesthetic cues. For these reasons, it might have been expected that in this position the nystagmus time constant would have been similar to that in the 30° forward position, but this was not found to be so.

For reorientations of up to 90°, therefore, the results were essentially of the expected form, and might be explained on the basis of either a peripheral or a central mechanism. The relatively small change in nystagmus time constant for displacements between 90° and 180°, however, cannot readily be explained in terms of either mechanism (Part I (1)). As with the preceding experiments, therefore, the findings do not distinguish between the role of peripheral and of central processes in the causation of the changes observed.

The results will be discussed in greater detail in Part 6.

PART 5

Section 5

Investigation of the Mechanism by which Gravity Modifies Post-Rotational Canal Responses

SECTION 5

INVESTIGATION OF THE MECHANISM BY WHICH GRAVITY MODIFIES POST-ROTATIONAL CANAL RESPONSES

Rationale of Experiment

The previous experiments in Part 5 have shown that the rate of decay of lateral nystagmus and the duration of after-sensations, following stimuli in yaw, were influenced by the position, or change of orientation of the subject with respect to the gravitational vertical, in the post-rotation period. The results of these experiments were inconclusive, however, so far as establishing with any certainty the nature of the primary mechanism by which gravity modifies post-rotational semicircular canal responses.

In a further attempt to elucidate the underlying mechanism, therefore, and to try to distinguish between the role of central as opposed to peripheral processes, an experiment was carried out using a situation in which the two hypothetical mechanisms (Part 1 (2)) predicted a different pattern of responses in the post-rotation period.

If a subject is rotated in yaw about a vertical axis,

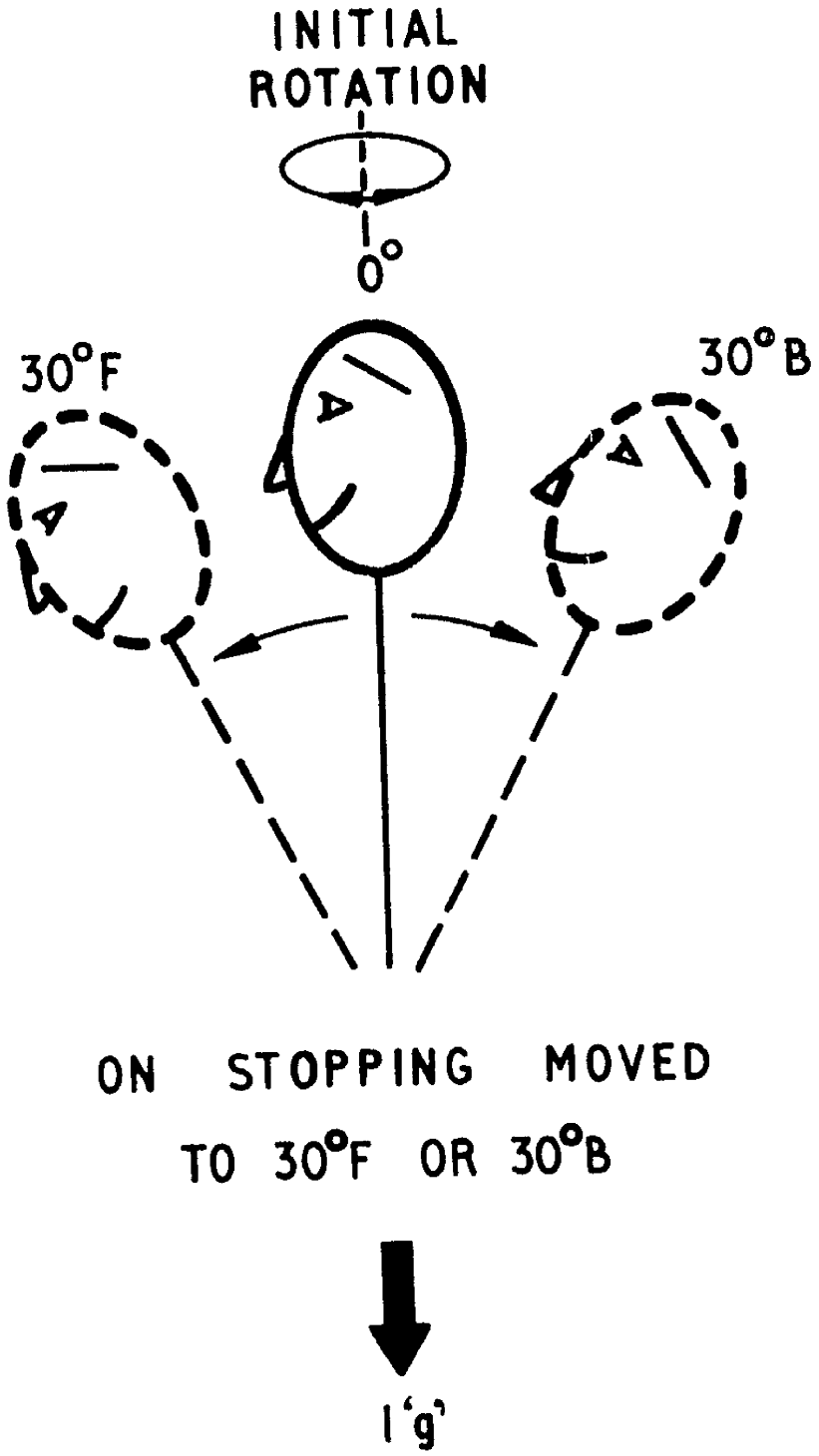


Figure 5.23

Diagram showing the 3 positions used in the experiment. The orientation of the plane of lateral semi-circular canals to the gravitational vertical is indicated by a short line in each position.

and on stopping tilted in the sagittal plane to a 30° forward or 30° back position, then the alignment of the plane of lateral canals to the gravitational vertical will differ by 60° in the two positions (Fig 5.23). The change in orientation of otolith and other gravi-receptor organs, however, and hence the somaesthetic information engendered, which will carry information that the signals from ampullary receptors of the lateral canals are inappropriate and should therefore be suppressed, will be essentially similar in each position. In these circumstances, if the magnitude of the g-vector coplanar with the stimulated canals can influence the rate of cupular restoration ('g on canal' mechanism), then on the basis of previous experimental results in Part 5, the nystagmus time constant of decay should be longer in the 30° forward position (lateral canals 90° to the g-vector) than in the 30° back position (lateral canals inclined 30° to the g-vector). Conversely, if 'somaesthetic inhibition' is responsible for modifying the inappropriate signals from canal receptors, the time constants in the two tilted positions should be equally reduced, with respect to the time constant if the subject remains in the vertical position.

METHOD

The experiment was performed using the turntable and variable position chair assembly already described (Part 5, Section 3), with the chair mounted so that it could be moved in the sagittal plane (Fig 5.10) between 30° forward and 30° back.

Twelve laboratory personnel (7 male, 5 female) acted as subjects.

Preliminary procedures were the same as those described in the previous experiment. The subjects were then rotated in yaw about a vertical axis, with the chair (and their head) vertical, and on stopping were tilted in the sagittal plane to either a 30° forward or 30° back position (Fig 5.23). They remained in these positions with their eyes closed for 30 sec, during which time they performed mental arithmetic as an 'arousal' task, while post-rotational lateral nystagmus was recorded by DC electroculography (Part 3 (3)). Calibration eye-movements were performed between successive runs.

There were six runs in this experiment, including controls in which the subjects were not moved from the vertical position in the post-rotation period. These were carried out with rotation both to the left and the right, and presented in random order according to a Latin-square design.

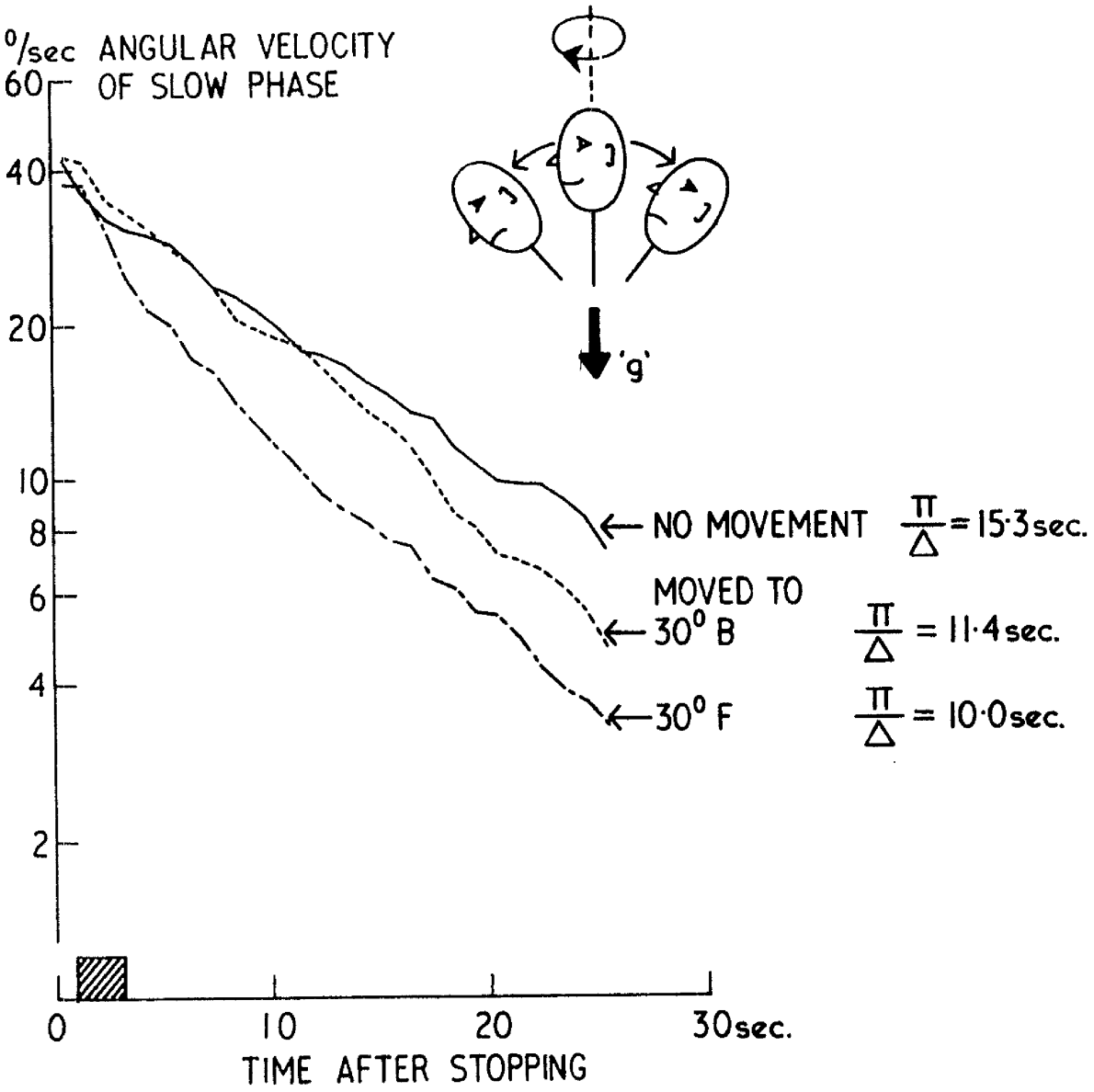


Figure 5.24

Comparison of the mean pattern of decay and time constant of nystagmus (π/Δ) in the 3 experimental situations, following rotation in yaw at 60°/sec about a vertical axis. Angular velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale. When subjects were repositioned, the shaded block indicates the period during which movement occurred.

RESULTS

The eye-movement records were analysed quantitatively (Appendix 1A), and a graphical representation of the mean pattern of decay of post-rotational nystagmus in each position (Fig 5.24) obtained in the manner previously described (Part 5, Section 1). The nystagmus time constant for the individual subjects in each position was also determined (Appendix 1B), and these values analysed statistically (Part 3 (8)).

The time constant of decay of nystagmus was significantly reduced ($p = 0.001$) both in the 30° forward (π/Δ 10.0 sec), and 30° back (π/Δ 11.4 sec) position, compared with the time constant when the subjects were not moved from the vertical (π/Δ 15.3 sec). The rate of decay of nystagmus was slightly greater in the forward than the back position, but there was no significant difference between the time constants in these two positions.

SUMMARY AND CONCLUSION

Following impulsive deceleration in yaw about a vertical axis, with the head upright, subjects were moved in the sagittal plane to a 30° forward or 30° back position. The time constant of post-rotational nystagmus was found to change with position, the nystagmus decaying significantly more quickly (shorter time

constant) when the subjects were repositioned (whether forward or backward), than when they remained vertical. There was no significant difference between the nystagmus time constants in the two tilted positions.

The similarity in reduction of the time constant of nystagmus following equal (30°) angular displacements from vertical, both in the forward and backward direction, although the alignment of the plane of lateral canals to the gravitational vertical differed by 60° in the two positions (Fig 5.23), implies that the orientation of the semicircular canals to gravity was not important in influencing post-rotational responses. Hence it seems unlikely that changes in the pattern (time constant) of decay of nystagmus were brought about by a direct action of the linear (gravitational) acceleration on the end-organ.

It has been emphasised already, however, that somaesthetic information, in conflict with inappropriate signals from the lateral canals, would be expected to be similar in the 30° forward and 30° back positions. The present results show a similar reduction in the time constant of nystagmus in these positions, compared with the vertical position in which somaesthetic signals would not conflict with those from the ampullary receptors.

It is concluded, therefore, that alterations in the pattern of post-rotational responses, according to changes in direction

of the gravitational vector, are mediated primarily through central processes, in which afferent signals from otolith and other gravi-receptor organs inhibit those from the ampullary receptors ('somaesthetic inhibition'), rather than by a peripheral mechanism involving changes in dynamic behaviour of the canal-cupula-endolymph system ('g on canal' hypothesis).

The findings provide the only direct experimental evidence in the present study to distinguish between these two hypotheses, as a general explanation for the principal mechanism underlying the post-rotational observations presented in Part 5.

The results and implications of this experiment will be considered further in Part 6.

PART 5

Section 6

Further Investigation of the Effects of Gravi-Receptor Input on Post-Rotational Responses in Yaw

SECTION 6

FURTHER INVESTIGATION OF THE EFFECT OF GRAVI-RECEPTOR INPUT ON POST-ROTATIONAL RESPONSES IN YAW

Purpose of Experiment

The previous experiment has shown that alterations in the pattern of post-rotational responses, following stimulation of the lateral semicircular canals, are governed primarily by the concomitant gravi-receptor input during the post-rotation period. That experiment, however, and the earlier ones in Part 5, investigated only the effect of position with respect to the gravitational vector, or of a single change in orientation of the subject immediately following the deceleration impulse. In these circumstances, therefore, the stimulus to gravi-receptor organs remained practically constant during the post-rotation period.

The purpose of the present experiment was to investigate the nature and consequences of the interaction between gravi-receptor and ampullary signals in more detail, by changing the gravi-receptor input in the immediate post-rotation phase. The experiment was confined to rotation in yaw about a vertical axis, and a sequence of two 90° post-rotation reorientations of the subject was used to alter the stimulus applied to otolith

and other gravi-receptor organs, and hence gravi-receptor input, during the post-rotational period.

Immediately following the stopping impulse (angular stimulus to the lateral canals), subjects were tilted to a horizontal position, and after 10 sec moved back to the vertical. Post-rotational eye-movements were recorded throughout, and from analysis of these records the effect of changes in gravi-receptor input on the nystagmus time constant of decay was determined.

METHOD

The experiment was performed using the turntable and variable-position chair assembly (Part 5, Section 3), with the chair mounted so that it could be moved in the coronal plane through $\pm 90^{\circ}$ (Fig 5.9 and 5.11).

Twelve laboratory personnel (6 male, 6 female) acted as subjects.

Preliminary procedures and the conduct of the experiment during rotation were the same as previously described. The subjects were rotated in yaw about a vertical axis, seated upright in the chair, and on stopping were moved immediately through 90° in the coronal plane to a left or right-side-down position. They remained horizontal for 10 sec, and were then moved quickly back to the vertical. Post-rotational lateral

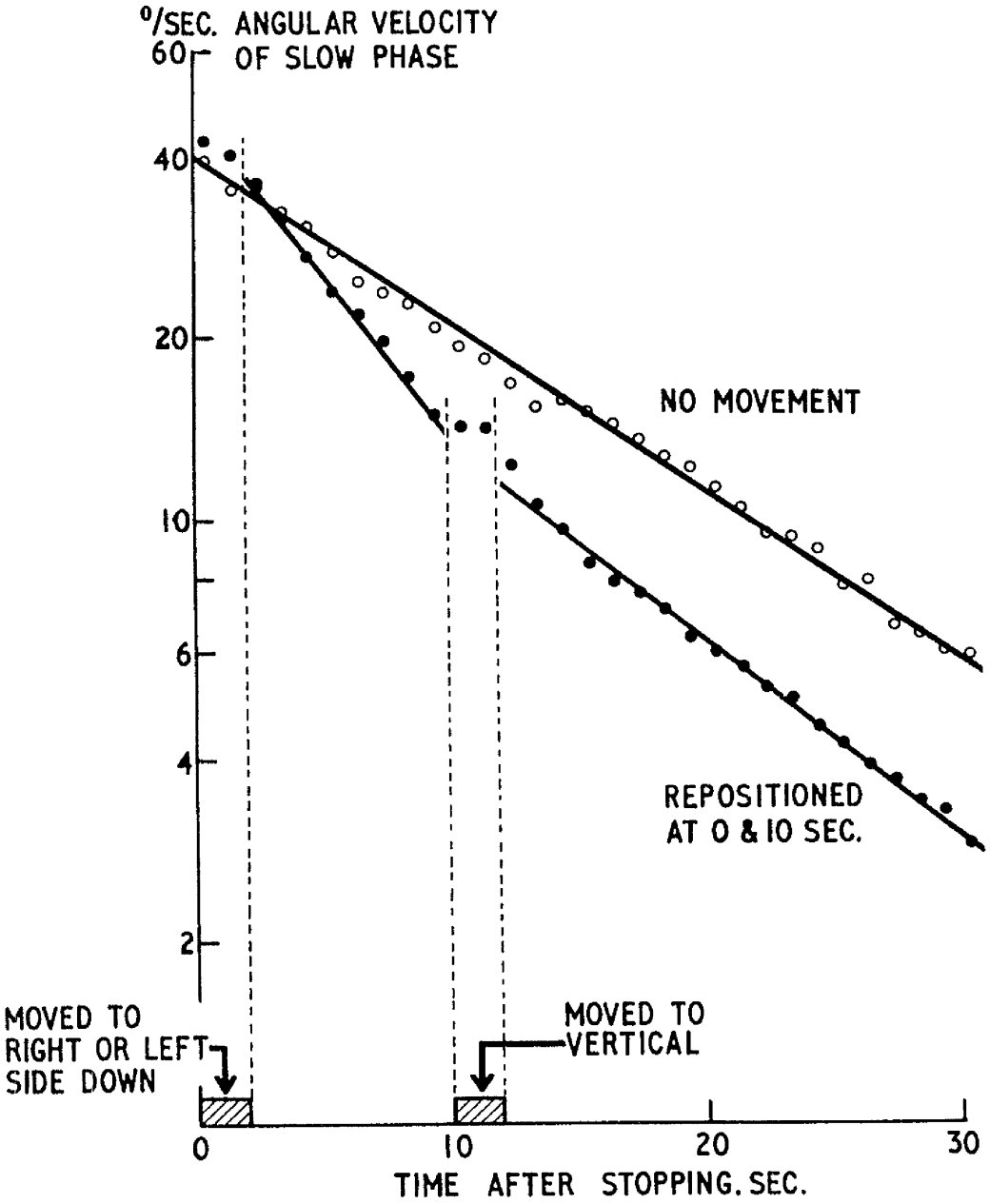


Figure 5.25

Comparison of the mean pattern of decay of nystagmus, evoked by impulsive deceleration in yaw from 60°/sec about a vertical axis, with the subject in different positions. Angular velocity of slow phase nystagmus is plotted on a logarithmic ordinate scale. Shaded blocks show the period during which subjects were repositioned as indicated. Based on results from 12 subjects.

nystagmus was recorded continuously, with the eyes closed, for 30 sec following the deceleration impulse, while the subject performed mental arithmetic. Calibration eye-movements were recorded after each run.

There were six runs in the experiment, including controls in which the subject remained vertical when the turntable was stopped, carried out for rotation in both directions, and presented in random order according to a Latin-square design.

RESULTS

The nystagmus records were analysed quantitatively (Appendix 1A), and the data from right and left-side-down positions combined (it has been shown previously (Part 5, Section 3) that there was no significant difference between the decay of nystagmus in these two positions) to give a graphical portrayal of the mean decay pattern of post-rotational nystagmus in each experimental situation (Fig 5.25), obtained in the manner described earlier (Part 5, Section 1). For statistical analysis, the time constants of decay for each subject in the different situations, were obtained from the calculated regression equation of the individual nystagmus plots (Appendix 1B). The mean values for each position are shown in Table 5.10.

TABLE 5.10

Position of Subject	Mean time constant (sec)
Vertical (no movement)	15.8
Moved to horizontal (Right or left-side-down)	7.9
Moved back to vertical	13.4

Mean nystagmus time constants in different situations

It can be seen from Fig 5.25 that the pattern of decay of nystagmus changed with the orientation of the subject to the gravitational vertical. When they were moved to horizontal, the rate of decay was increased to a level similar to that observed in an earlier experiment (Part 4, Section 3). But when the subject was restored to the vertical position after 10 sec, although there was no appreciable change in the magnitude of the slow phase velocity at the time of movement, the subsequent rate of decay of nystagmus was reduced.

As in the earlier experiment, the reduction of time constant when subjects were moved from vertical (π/Δ 15.8 sec) to the horizontal (mean π/Δ 7.9 sec) was highly significant ($p= 0.001$). The increase in time constant to 13.4 sec, when they were returned to vertical, was also significant ($p= 0.01$), although this value was lower ($p= 0.05$) than the time constant obtained when the subjects were not moved from the vertical position in the control runs.

SUMMARY

Following stimuli in yaw about a vertical axis, subjects were moved in the coronal plane to a horizontal (right or left-side-down) position, where they remained for 10 sec and were then returned to the vertical.

The rate of decay of post-rotational nystagmus changed with the orientation of the subject to the gravitational vector. The time constant of decay was reduced following movement to the horizontal position, and increased again after the subject was returned to vertical. There was no appreciable alteration in the magnitude of the slow phase velocity of nystagmus at the time of movement.

These results are in accord with a 'somaesthetic inhibition' mechanism, as suggested in the previous section, and also demonstrate that changes in the rate of decay of post-rotational nystagmus mediated in this way are rapidly reversed if the inhibitory gravi-receptor information is removed.

It is concluded from these findings that the change in intensity of the inhibitory signal must have the form of a complex variable, rather than of a simple subtractive or proportional alteration in the ampullary signal, for either of these latter mechanisms would have produced a sudden change in nystagmus velocity, coincident with the appearance of competing gravi-receptor signals when the subjects were repositioned, and this was not observed. In addition, proportional inhibition would not appreciably alter the rate of decay of nystagmus, but simply 'displace' the log-linear velocity-time graph to an approximately parallel position, so that the time constant would ramain practically unchanged.

The results will be discussed in greater detail in Part 6, with special reference to the nature of the inhibitory gravi-receptor signal.

PART 6

GENERAL DISCUSSION

PART 6

GENERAL DISCUSSION

1. Background Factors

The specialised vestibular receptors provide information about accelerative motion in space and with respect to the gravitational vertical. With evolution the dynamic responses of this system have become optimised for the environmental circumstances encountered. Man, however, has developed artificial aids to motion and experimental situations which expose him to patterns of acceleration differing in magnitude and time course from those to which his vestibular system is functionally designed. On exposure to such unnatural circumstances, therfore, the vestibular system generates erroneous information. This leads in turn to illusory sensations and inappropriate reflex responses which may cause uncertainty or 'disorientation'.

This study presents a background review, and an account of a series of experiments which are thought to be relevant to these realms of uncertainty. What follows is a brief discussion bearing on the significance of the experiments described.

It should not be surprising, however, that though many factors are considered, few concrete conclusions can at present be reached on the basis of currently available evidence. For in any fundamental studies, the anatomical and functional differentiation of the vestibular apparatus has led to a dichotomous approach (Benson, 1970). In consequence the precision with which separate responses to angular and linear accelerations can now be described (Young, 1968; Melvill Jones, 1970) has not, hardly surprisingly, been matched by equal certainty with respect to the mechanisms whereby the numerous laboratory observations can be reconciled and explained.

2. Per-rotational Findings

The experiments described in Part 4 demonstrate unequivocally that the pattern of per-rotational nystagmus was altered by the concomitant linear acceleration vector. In both Yaw (section 1) and Pitch (section 2), continuous compensatory nystagmus (i.e. with slow phase component in the opposite direction to that of the angular motion) was present for the duration of rotation at constant velocity.

This cannot be explained by the classical hydrodynamic theory of canal behaviour (Mach, Brown, 1875; Breuer, 1874) which attributes nystagmus to deflection of the cupula mediated by dynamic cupular changes imposed by the effects of

the initial angular acceleration of the endolymph. The initial high peak nystagmus velocity, which does show some exponential decay over the first few cycles of rotation (Fig 4.6) might be explained in this way, but not the sustained nystagmic response thereafter, which, IF it is cupular in origin implies a persistent cupular deflection. In fact the cupulae of the canals in the plane of rotation should return to a central position at a rate determined by their intrinsic restoring couple and the viscous damping of the endolymph. The angular velocity of slow phase nystagmus is thought to be related linearly to cupular deflection, and therefore to the rate of discharge of ampullary receptors, so that nystagmus should decay with an exponential time course until it is no longer discernible.

It has been shown that for rotation about a vertical axis, both in yaw and pitch where the relation between the stimulated canals and the gravitational vector remains constant, this indeed occurs (Part 3, section 2). But once the nystagmus elicited by an angular acceleration has died away, continued rotation at constant velocity should not produce further nystagmic responses. The experimental findings during horizontal axis rotation, therefore, require an explanation either in terms of modification of the classical concept of canal behaviour, or by some different mechanism engendering

signals which interact with those from the ampullary receptors.

De Kleijn and Magnus (1921) thought the canal receptors could respond to linear acceleration, and this theory gained support from experiments in the frog (Ledoux, 1949) and cat (Gernandt, 1950) where responses of ampullary receptors were shown to be modified by changes in the magnitude and direction of the linear acceleration to which they were exposed. Likewise, the centrifuge experiments of Benson and Whiteside (1961) led to a similar conclusion, though this study may be criticized on the grounds that the linear acceleration was 'unphysiological' (3.1g). Again, McLeod and Correia (1964) using caloric stimulation concluded that the cupulae were gravity sensitive, though Benson (personal communication) has criticized their findings.

Collectively these studies provided a body of evidence which suggests that the cupula might be gravity sensitive, and as a logical corollary that it would also require to be of greater density than the endolymph. If this were true, the cupulae of the lateral canals would be deflected in a direction to produce 'horizontal' nystagmus in one direction when the subject lay, say on their right side, and in the opposite direction when rotation through 180° occured (i.e. left side down position). This was not observed. In general also it may be shown that in these circumstances effective cupular

deviation (i.e. the difference between ampullopetal deflection in one canal, and ampullofugal deflection in the contra-lateral canal) is theoretically proportional to the sine of the angle of deviation of the sagittal plane of the skull from the gravitational vertical. This implies that a true positional nystagmus (Stenger, 1955) should occur (i.e. as opposed to nystagmus elicited by change of position) but only two subjects showed such nystagmus, and in only one did it occur in the predicted directions (Table 5.2).

Whatever the mechanism, it would appear that if the cupula is directly deflected by a static linear acceleration of 1g this is not, in most normal individuals, an 'adequate' stimulus to the ampullary receptors.

The work of Money (Part 2), however, suggesting that a significant difference in density between endolymph and perilymph was unlikely, together with observation that the cupula and endolymph have the same refractive index (Howard and Templeton, 1966), prove major stumbling blocks to these theories. The present consensus of opinion is strongly against the cupula being influenced <u>directly</u> by gravity or other linear accelerations. In the present experiments, for example, a 'g sensitive' cupula would be expected to give a consistent direction changing nystagmus during sustained rotation, and this was not observed. Similarly, as noted, spontaneous

nystagmus of opposite sign might have been anticipated as a regular finding in different 'static' positions, but again this was not found.

A direct 'g on cupula' effect is not the only mechanism, however, which could account for the experimental observations. Aside from central interaction and otolith effects (discussed later), and the consequences of efferent innervation of the sensory cells of the crista(Engstrom, 1958), a 'g on canal' hypothesis (quite distinct from limited 'g on cupula' mechanisms) based on the possible deformation of a non-rigid fluid filled 'ring', allows an alternative explanation for the per-rotational experimental findings.

If a change of pressure distribution within the canals occurred under the influence of a linear acceleration, this might bring about deflection of the cupula. Stenger (1955) suggested that the hydrostatic pressure is greater in the dependent labyrinth. This could only cause differential movement of endolymph in the semicircular canal, with concomitant cupular deflection, however, if small changes in volume of either the endolymphatic or perilymphatic spaces could occur. Otherwise there would be only an equal and opposite pressure difference across the cupula, which would not produce a deflection.

It has been postulated (De Kleijn and Magnus, 1921)

that the round or oval windows might provide a degree of compliance, which would fulfil the necessary requirements, and with the aid of models shown that deflection of 'the cupula' can be produced by linear acceleration. However, prima facie a mechanical system of this sort would be expected to deflect the cupula in the same direction as that which would occur if the cupula were of greater density than endolymph. It would not appear capable of producing a sustained unidirectional cupular deflection in the presence of a continuously rotating coplanar linear acceleration vector, as the present observations would require.

The emphasis so far has been by implication on the lateral semicircular canals, because relatively these form a simple system on which the hypothetical effects of a revolving 'g' vector may be considered in comparative isolation. The vertical canals, because they are paired structures inclined at about 45° to one another, present a more complex situation, though it is considered that the hypothetical arguments under discussion may be applied equally in principle to these structures (Bodin, 1968).

If we discard the mechanisms above as an explanation of the presence of sustained nystagmus, the possibility remains that some comparable mechanism might underly the presence of

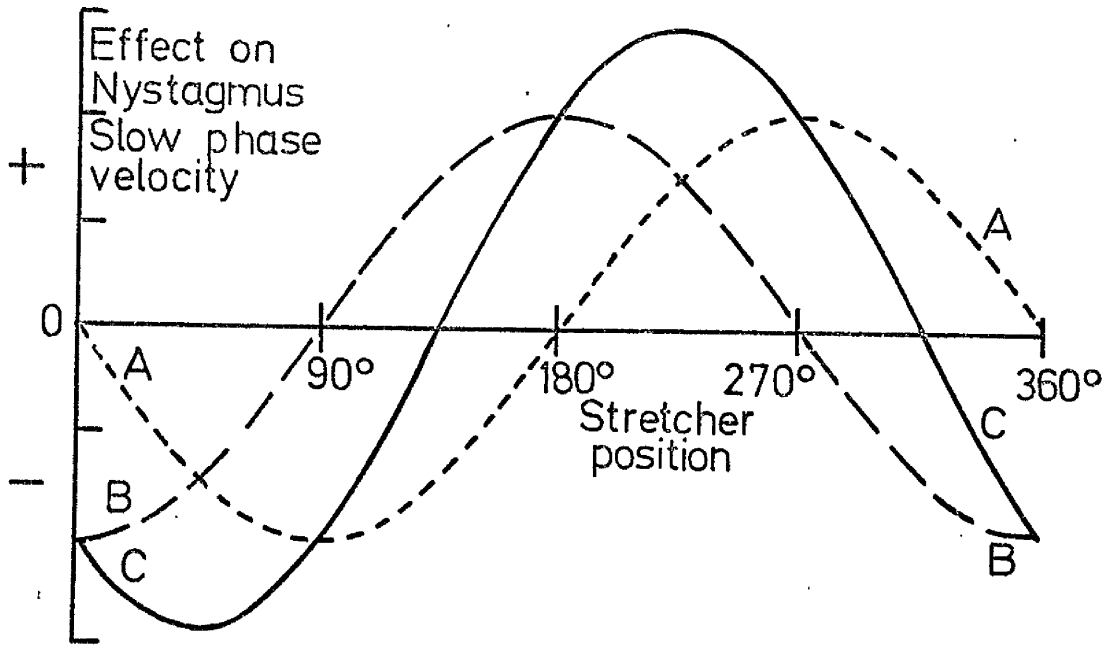


Figure 6.1

Theoretical modification of nystagmus slow phase velocity by signals from ampullary receptors (A) if cupula position is influenced by the direction of the linear acceleration, and from the otolith organs (B). C is the algebraic sum of A and B.

sustained nystagmus, or even the cyclical modulation of nystagmus velocity observed in both experiments during 'steady state' rotation at constant speed. For, in the 'rotating stretcher' experiment for example, the modulation would be expected to follow a sinusoidal time course with a minimum velocity in the 90° position and a maximum at 270° (Fig 6.1), which is not dissimilar to the assymetric sinusoidal nystagmus velocity plots shown in Fig 4.13.

Such a mechanism may be postulated on the basis of the observations of Money and James (Part 2), from which it can be concluded that the membranous canal with contained endolymph differs in density by a significant amount from that of the perilymph. Also, since it is not a rigid structure (Lorente de Nó, 1931) and occupies only one third of the space within the bony canal, it could undergo slight movement or deformation within the bony canals. Such a hypothetical deformity, when a '1g' linear acceleration vector acts across the plane of the canal, is shown diagramatically in Fig 6.2. The membranous canal becomes narrowed by compression against the wall of the bony canal at its 'highest' point. As the coplanar vector rotates, so the area of compression moves round the wall; the endolymph inside is 'milked' round the canal in such a way as to produce a continuous redistribution of internal hydrostatic pressure,

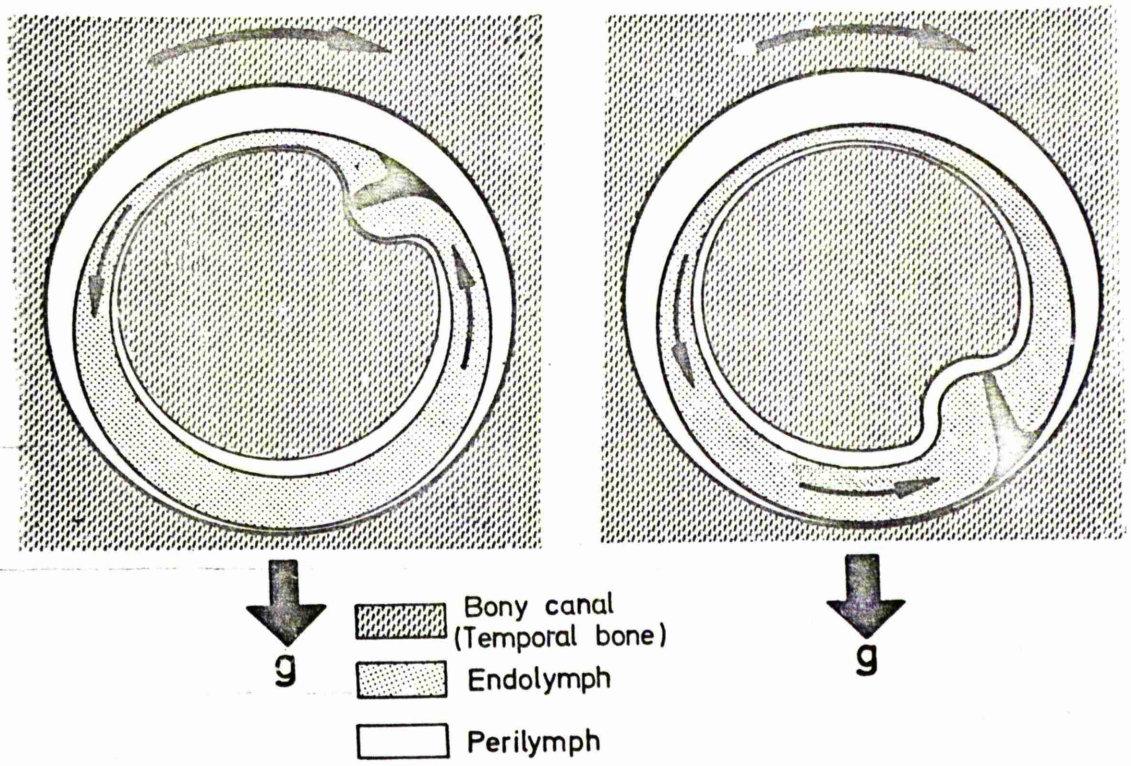


Figure 6.2

Conjectural diagram representing the change in position and shape of an idealized membranous canal within a bony canal during clockwise rotation. From above down the arrows show direction of rotation, endolymph flow, and force due to gravitational acceleration (g).

related to the velocity of rotation of the vector, and consequently sustained unidirectional cupular deflection with compensatory nystagmus. This hypothesis, in which 'g' alters the dynamic behaviour of the canal-cupula-endolymph system, will be termed the 'g on canal' mechanism.

Following deflection of the cupula by an angular acceleration in the plane of the canals, its subsequent restoration would be determined only by the opposing forces of viscosity and the intrinsic restoring couple of the cupula. A sustained change of hydrostatic pressure within the canal, therefore, would not affect the rate of cupular return, but only its final equilibrium position (which would be displaced from the normal resting position by an amount related to the pressure differential across the cupula). Thus, the rate (time constant) of decay of per-rotational nystagmus immediately following an angular acceleration, should be the same in the vertical as the horizontal axis (i.e. independent of the coplanar 'g' vector) - a prediction substantiated by the experimental results (Fig 4.6) - while in the latter situation full cupular restoration would be prevented from occurring, and sustained nystagmus engendered, with a mean velocity of slow phase related to the degree of residual cupular displacement.

Despite what has been said above, it is not easy to

explain the sinusoidal pattern of nystagmus modulation by such a mechanism. It seems unavoidable to evoke a secondary hypothesis to account for it. No primary canal process appears able to do so for one is reluctant to postulate, without any substantiating evidence, a direct effect of the linear acceleration producing in some way small cupular oscillations about the position of mean displacement. Here it is logical to turn to the other vestibular end-organ specifically receptive to linear accelerations, namely the otolithic maculae. Theoretical nystagmus velocity changes for the otolith alone, and due to combined interaction between canal and otolith mechanisms, are shown in Fig 6.1. It is notable that the pattern, in respect of shape, is similar to that in Fig 4.13, but whereas theory predicts a reversing nystagmus, this was not observed in practice. It may be, however, that the primary cupular mechanism simply determines a 'base line' sufficiently far above zero for subsequent oscillatory changes not to produce reversal, except possibly at the very lowest velocity, e.g. Figs 4.14 and 4.15. Note that at very low velocities the whole pattern of modulation is altered and inconsistent between subjects.

Since the 'g on canal' hypothesis was evaluated by the writer in 1964 (Benson and Bodin, 1965, 1966) a number of other studies have been carried out on the phenomenon of nystagmus

evoked by continuous rotation of a 'g' vector coplanar with the lateral canals. These have essentially confirmed the original experimental observations, but leave open or cast serious doubt on the hypothetical explanation proposed here.

Guedry (1964) independently carried out the 'rotating stretcher' experiment, with essentially similar results to those described here. He concluded, in the absence of evidence that the cupula was gravity sensitive, that the findings were almost certainly due to interaction between signals for ampullary receptors, and those from the otoliths. Later, Benson, Guedry and Melvill Jones (1967) studied the electrical activity of neural units in the vestibular nuclei with stereotactically implanted electrodes. These experiments used cats, subjected to rotation with a centripetal acceleration of 0.42g on a parallel swing (i.e. pure ~~angular~~ LINEAR without ~~linear~~ ANGULAR motion); units responding only to angular acceleration in the horizontal plane were studied. The findings were considered to support the 'g on canal' hypothesis.

In contrast, Benson (1968) studied the effects of rotating linear acceleration vectors less than 1g, coplanar with the lateral canals, using human subjects seated on a counter-rotating platform on the arm of a miniature centrifuge. Both sinusoidal eye movements and direction changing nystagmus were

observed, each of a compensatory nature; the former were considered appropriate to a sustained re-orientation to the acceleration vector, and the latter to translational motion in the lateral direction. It was considered that the results were more probably caused by stimulation of otolith and other somaesthetic receptors, than by a change in the dynamics of the canal-cupula-endolymph system. The findings and conclusions were in general agreement with those of Niven, Hixon and Correia (1965) for nystagmus evoked by sinusoidal motion on a horizontal track.

The most important recent studies, however, have undoubtedly been those of Correia and Money (1968) and Janeke (1968). The former workers repeated the experiments described in Part 4 using cats. They showed that following surgical transection and blocking of all six semicircular canals, horizontal and vertical responses to angular acceleration about an earth-vertical axis were abolished. Nystagmus during constant velocity rotation about an earth-horizontal axis remained, however, though the pattern of slow phase eye velocity was altered. From this it was concluded that continuity of semi-circular canals, though perhaps contributory, was not necessary for nystagmus during constant velocity horizontal-axis rotation.

Janeke also used surgical methods. Partial labyrinthectomy

was performed in rabbits, in which the otolith organs were destroyed and their nerves severed, but the canals left intact. Eye movements and nystagmus during horizontal-axis rotation were completely abolished. The integrity of the canals was confirmed by torsion swing tests. He concluded that the eye-movements and concomitant nystagmus both originate from the otoliths. In a further experiment, Janeke was able to provoke nystagmus by direct mechanical stimulation of the utricular macula, while cupular activity could be excluded.

Most of the workers who performed these studies are known personally to the writer, as scientists of ability and integrity. Due weight may be placed on their findings, therefore, and it is concluded that the 'g on canal' hypothesis expounded earlier, which already makes considerable unsubstantiated assumptions about the dynamics of the canal-cupula-endolymph system, must largely be discarded as untenable.

A number of workers have suggested the possibility that the otoliths may modulate the sensory input from the ampullary receptors of the canals (Tait and McNally, 1934; McNally, 1955; Lowenstein, 1956; Miodonski, 1962), but it was Guedry (1964) who first proposed this hypothesis as an explanation for the continuous lateral nystagmus observed during earth-horizontal cephalo-caudal body axis rotation. Guedry did not elaborate on

his suggestion, but only put it forward as the most likely possibility, in his view, having discarded 'g on cupular' mechanisms. He did, however, note that constant reorientation of the body to gravity involves widespread stimulation of other proprioceptor end-organs, and for subsequent discussion these will be considered together with the otoliths as the 'somaesthetic hypothesis'.

Beyond attributing the experimental observations in Part 4 to somaesthetic (primarily otolith) causes, it is not possible at present to expand upon the role of different operative factors, or formulate a mathematical model. Insight into these aspects can better be gained from the post-rotational experimental findings, though how relevant any 'model' constructed on post-rotational observations is in detail, as opposed to general principles, to per-rotational findings, cannot be said. Nevertheless, it is convenient to defer further discussion of these points to the final section.

3. Post-rotational Findings

One of the main findings in the experiments described in Part 5 was that post-rotational responses, in all three axes, depended significantly on the position, or change in orientation of the subject, with respect to the gravitational vector. Essentially the same differences were observed when responses

following rotation about fixed orthogonal axes were compared (sections 1 and 2), as when the subjects were rotated about a vertical axis and repositioned through 90° in the immediate post-rotation phase (section 3). The final three sections essentially examined intermediate 'situations', suggested by the earlier experiments, in an attempt to clarify the nature of the changes and of possible responsible mechanisms.

Most of these experiments were concerned with the reduction of post-rotational responses when the gravitational vector was coplanar, compared with when it was normal, to the stimulated canals. In the first experiment, however (section 1), differences related primarily to the direction of the vector when it lay in the plane of the lateral canals were examined. During continuous horizontal axis rotation in Yaw (Part 4, section 1), cyclical modulation of nystagmus velocity was observed, with a minimum in the right-side-down (90°) and a maximum near the left-side-down (270°)positions. From this it might have been expected that post-rotational responses would show a similar dependence on position, with a greater time constant and peak nystagmus velocity in the 90° than the 270° position (Fig 5.1). However,although nystagmus velocity was found to be higher in the 90° than the 270° position, a similar difference was present between the velocity in the 0° and 180° positions,

while the time constants did not differ significantly in the four positions. One possible inference is that cupular deflection makes only a partial contribution to the sustained per-rotational nystagmus, but in general it may be concluded that the direction of the linear acceleration, when coplanar with the lateral canals, was unimportant in regulating cupular restoration.

This need not necessarily conflict with a 'g on canal' hypothesis for production of per-rotational nystagmus, for it is possible that on cessation of rotation, equilibrium of the linear acceleration mechanism would be rapidly restored, the cupula deflected only by forces produced by the stopping impulse, and uninfluenced by any associated with the linear acceleration vector. It lends no support to such a hypothesis, however, and indeed it seems unlikely that the reduction of post-rotational responses in horizontal positions, compared with those in the vertical axis, can be explained on this basis, in terms of alteration of canal dynamics by a direct effect of the linear acceleration. In the static situation, such a mechanism would require considerable assumptions about the configuration of the membranous canal, in relation to the gravitational vertical, which have no evidence to substantiate them; while the finding in most experiments that reductions

in after-sensations, often proportionately greater than the decrement in the corresponding time constant, were associated with changes in sensory thresholds, suggests a central rather than a peripheral mechanism.

In general, it is considered that aberrations in post-rotational responses were most probably due to central processes in which signals from otolith and other gravi-receptors, engendered by differences in orientation to the gravitational vector, interact with those from the ampullary receptors. Certainly, in the post-rotation period, somaesthetic signals would carry information that the body was not turning, which would be expected to conflict with and inhibit the inappropriate signals from semicircular canals. Such a hypothesis receives strong support from the experiment in which subjects were moved 30° forward or back from the vertical position (section 5), while the same results argue against a 'g on canal' mechanism in these circumstances.

In the experiment which compared post-rotational responses following stimuli in Pitch about vertical and horizontal axes (section 2), no significant difference was found between the time constant of nystagmus in the two axes. This was in contrast to the findings in most of the other experiments in Part 5, and particularly those from Section 1 (discussed above) in which a

similar comparison was made in Yaw. However, following horizontal axis rotation, there was a considerable reduction in after-sensations, compared with those in the vertical axis, for stimuli both in Pitch and in Yaw. From these observations it may be inferred that in the horizontal axis, while there was an appreciable change in sensory threshold in both Pitch and Yaw, the inhibition of ampullary signals passing to the vestibulo-ocular pathways, by those from somaesthetic receptors, was considerably greater after rotation in Yaw than in Pitch. A possible explanation for this difference may be the fact that, whereas normal (rotational) head movements in Yaw are not generally associated with an appreciable alteration in gravi-receptor input, movements in Pitch are always accompanied by a change in otolith signal. Hence, it might be expected that in Pitch, where interaction between canal and otolith information is "physiologically familiar", there would be less inhibition of inappropriate ampullary signals, than in Yaw where concomitant changes in these two sensory inputs are unusual (Bodin, unpublished observations).

It is less easy to account for the difference in time constant following forward and backward rotation in Pitch in the horizontal axis, for the subjects were always stopped in the vertical position, so that somaesthetic information would be

expected to be similar each time. Also, for rotation in Pitch about a vertical axis, there was no difference between the duration of after-sensations in those situations, or between the time constants or after-sensations for rotation in the two directions. No simple explanation can be given for these differences.

The experiment in which subjects were repositioned through 90°, following vertical axis rotation in each of the three orthognal planes (section 3), demonstrated a much greater reduction in after-responses for stimuli in Yaw, than in Pitch or Roll. It is not so easy to explain this finding on the basis of a central inhibitory mechanism. Melvill Jones, Barry and Kowalsky (1964) attributed differences between after-responses in Yaw and in Pitch and Roll, to inherent differences in the dynamics of the lateral and vertical canals. This may in part have been brought about by the differing orientation of the lateral and vertical canals to the gravitational vector during rotation; for whereas the magnitude of the coplanar acceleration vector in Yaw changed by approximately 1g, in the vertical canals (Pitch), because of their 45° inclination, the corresponding change would be only $\frac{1}{\sqrt{2}}$ g. Whatever the reason, they cannot be attributed to differences in dimensions of the canals, which are negligible (Melvill Jones, personal communication).

Nevertheless, in the present experiment the change in magnitude of the coplanar 'g' vector, for a 90° reorientation of the subject, was much greater in the lateral than the vertical canals; a change which correlated with the observed alterations in after-responses. On this basis, a change in canal dynamics might seem to offer an easier explanation than 'somaesthetic inhibition', and indeed otolith and other gravi-receptor organs would be likely to provide similar information about the absence of bodily rotation in Yaw, when the subjects were moved from upright to the horizontal, as in Pitch and Roll when they were moved from horizontal back to the vertical position. However, it might also be argued, since "normal" after-responses for vertical axis rotation are appreciably less in Pitch and Roll than in Yaw, that for a similar increase in gravi-receptor information, the decrement in responses would be smaller in Pitch and Roll than following rotation in Yaw.

Irrespective of the responsible mechanism, however, these observations have relevance to problems in aerospace medicine, which it is convenient to interpolate at this point in the general discussion. Illusory sensations of turning arising from inappropriate vestibular signals are a frequent cause of spatial disorientation in flight, and an understanding of the dynamics of the canal-cupula-endolymph system is of value in the prediction

of the time course and magnitude of such illusory sensations both during and following angular motion in flight (Melvill Jones et all, 1964). Unfortunately, the demonstration that the constants which describe the dynamics of this sensory system are not fixed, but vary with the direction of the linear acceleration, means that the sensory sequelae of a particular flight manoeuvre cannot be predicted by consideration solely of the angular motion, but must also take into account the direction and magnitude of the concomitant linear acceleration vector. The picture is further complicated by the fact that the threshold in this sensory modality is not stable, but alters considerably according to the pattern of stimulation of both the vestibular and other somaesthetic receptors.

As the rate of decay of inappropriate post-rotational responses is greater when the linear acceleration is coplanar with the stimulated canals, and least when normal to the plane of the canals, it is theoretically possible for the aviator to accelerate the decay of erroneous sensations if he is able to align his head appropriately to the prevailing linear acceleration vector. However, apart from the practical difficulties of executing such manoeuvres it is not axiomatic that disorientation would be ameliorated, for the pilot may well be more disturbed by the change in the plane of rotation and the intensity

of the sensation which can occur with reorientation of the head to the acceleration vector (Purkinje and/or Coriolis effects).

Extrapolation of the observations made in the presence of gravitational acceleration to the weightless state is not without considerable limitations, though from the present experiments it may be inferred that in the zero 'g' environment the dynamic responses of the canal system would differ from those observed on the surface of the earth (Bodin, 1966). If linear acceleration modifies canal function at the end organ, then the time constant of cupular restoration should be less under weightless conditions than at 1g. However, if otolith and other gravi-receptor cues are of aetiological importance, then it is likely that the time constant would be greater in the weightless environment (Benson and Bodin, 1966).

So far only experiments involving 90° changes of alignment to the gravity vector have been considered. Section 4 was therefore designed to examine intermediate situation ('multi-position experiment', Bodin, unpublished observations). The experimental results, for post-rotation reorientation to five different positions between 30° forward and 150° back (i.e. over an arc of 180°), following stimulation of the lateral canals

by rotation in Yaw about a vertical axis, have been collated in the terminal 'summary' of section 4.

The anomalous finding in this experiment is that the pattern of decay for positions in the quadrant below horizontal are quite different to those above the horizontal (Fig 5.22), though the alignment of the body and semicircular canals to the gravity vector are the same. This cannot readily be explained either by 'g on canal' or a 'somaesthetic' hypothesis, although in favour of the latter it may be argued that gravi-receptor input would be quite different when the subject was hanging in their straps in the inverted position, compared with that in the 0° to 90° quadrant when they were not. On the whole, however, this experiment provides little more than an 'elegant demonstration', but is not really helpful so far as the basic underlying aetiological mechanism is concerned.

By contrast, however, the '30° forward, 30° back' experiment in section 5 was specifically designed to examine the underlying mechanism of the post-rotational experimental observations, in an attempt to differentiate between the role of a possible 'g on canal' mechanism, and that of 'somaesthetic inhibition'. The underlying theory, results and conclusions have already been fully described (section 5, 'Summary'), and the findings seem unequivocal; there can be little doubt

that in this experimental situation, somaesthetic inhibition of signals from the ampullary canal receptors is the principal aeteological mechanism. It seems not unreasonable to extrapolate from this and postulate that such a mechanism also underlies most of the other post-rotational observations in Part 5.

The final experiment (section 6) was designed in the light of the findings of the previous section, to try to elucidate the nature of the inhibitory mechanism and to enable a tentative mathematical 'model' of the possible underlying theoretical principles to be formulated. The experimental observations and some tentative conclusions have already been summarised; these will now be expanded.

It may be noted, en passant, how quickly the pattern of slow phase nystagmus velocity decay changed when subjects were moved from the vertical or horizontal positions, and how readily these changes were reversed when the initial orientation of the subject was restored. The otolith is clearly not a sluggish organ, as sometimes supposed, but capable of quick, almost immediate, response, when the forces acting on it are changed. This is a valuable observation, as a rapid response time is a prerequisite for any mechanism if it is to adequately explain the findings in the present study.

Let us postulate in general that the post-rotational observations in Part 5 are mediated by some form of gravi-receptor or 'somaesthetic inhibition' mechanism. The basis for this supposition has already been outlined in principle. Likewise the main factors which have to be taken into account have also been considered in general terms. Persuing this hypothesis, we are now in a position to lay down certain theoretical fundamental considerations, noting features which are inconsistent with the findings and must be disregarded as untenable, as well those which have to be given positive consideration and may be formulated in mathematical terms.

It is clear from the last two experiments that the inhibition of ampullary signals from the stimulated semicircular canals cannot be a simple subtractive, proportional change or alteration in 'gain' of the system, for with any of these a sudden 'step' fall in nystagmus slow phase velocity would have occurred, and the nystagmus decay with the same time constant irrespective of the intensity of the inhibitory signal, coincident with the appearance of competing gravi-receptor information on re-orientation of the subject. Furthermore, any proportional inhibition would not alter the rate of decay of nystagmus, but simply "displace" the slow phase velocity-time graph to a parallel position (i.e. with the same time

constant). No sudden change in nystagmus velocity was observed, but only an alteration in the subsequent rate of decay (slope of the velocity-time plot - Fig 5.25). Accordingly, these considerations lead to the conclusion that the intensity of the basic inhibitory signal must increase as an exponential function of time, with the exponent itself a function of the gravi-receptor signal. This may be described by a general equation, illustrating a possible efferent signal from mid brain to higher vestibular centres, of the form:

$$E = Ae^{skt}$$

where
- E = intensity of the efferent signal to higher vestibular centres.
- A = intensity of ampullary afferent signal.
- s = intensity of somaesthetic signal, changing with respect to time.
- k = an arbitary constant which determines the differing degrees of inhibition for nystagmus and sensations of turning, which have appreciably different time constants for the various manifestations of post-rotational responses.
- t = time after stopping.

In other words, to agree with the results of the last two experiments, the primary requirement is that the inhibitory

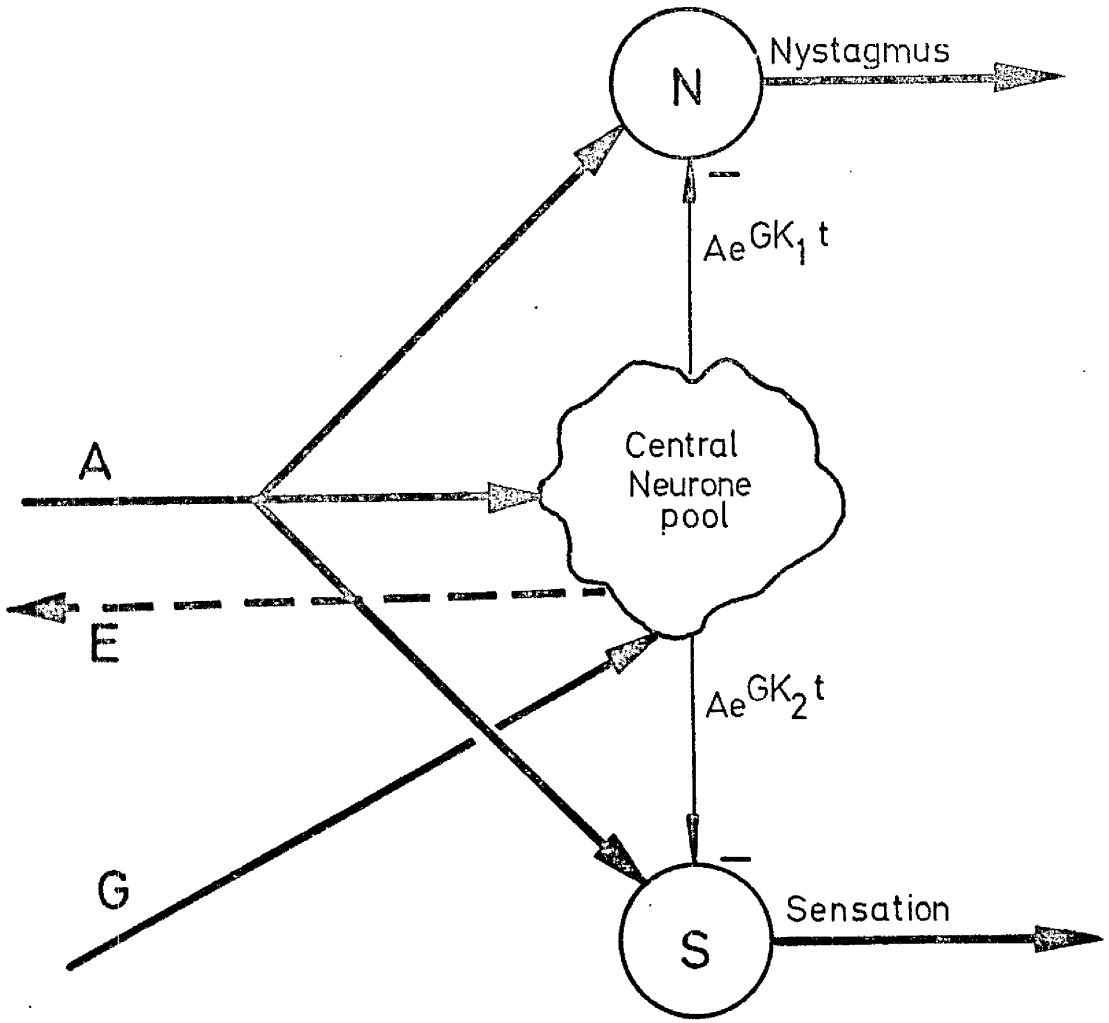


Figure 6.3

Conjectural diagram of interacting neuronal pathways in the 'vestibular centre' of the mid brain. Affarent signals (A) divide to innervate subsidiary centres subserving nystagmus (N) and sensations (S) which experimentally have different time constants. Gravireceptor (G) is used in place of somaesthetic input to avoid confusion with sensations. The time constants of signals from the subsidiary centres are altered by virtue of the differing inhibitory signal which each receives (see main text, page 160). Efferent signals (E) pass back to the peripheral end organs; their influence is uncertain, but would be likely to effect nystagmus and sensations to a comparable, rather than a different, extent.

signal increase in magnitude as an exponential function of time, with the exponent itself a function of the intensity of the input from somaesthetic (particularly otolith) receptors.

Such an equation represents only the simplest basic principle which might be involved. Any mathematical 'model' based on this equation must inevitably be more complex, to allow for the fact that different indices of vestibular function, e.g. nystagmus and sensations of turning, decay at dissimilar rates, and must therefore experience differing degrees of inhibition. The role of an efferent 'feed back' to the ampullary end-organ must also be considered. A simple schematic diagram embodying these principles (with no anatomical implications) is illustrated in Fig 6.3.

Many alternative mathematicl 'models' might be proposed, but here it is intended only to present one such 'model', illustrating the fundamental principles consistent with the experimental observations. There is really no evidence to allow elaboration of this or alternative hypotheses at the present time, and the simplicity of the proposed 'model' serves only to illustrate our present inadequacy in the field of basic vestibular physio-anatomical mechanisms.

Further advances may well only be made by more detailed animal experimentations involving both surgical procedures on

the end-organ receptors, and recording from the vestibular nerves and mid-brain centres of 'intact animals', than have hitherto been made. Useful advances in elucidating the complexities of basic vestibular mechanisms will likely require the joint co-operation of physiologists, anatomists, neurologists, otologists, physicists and computers, and must await the course of time.

PART 7

CONCLUDING REMARKS

PART 7

CONCLUDING REMARKS

The results of this study demonstrate conclusively that vestibular responses to angular motion, both during and after rotation in Yaw and Pitch, and the pattern of post-rotational responses in Roll, were significantly altered by changes in the concomitant linear acceleration. During continuous rotation in Yaw and Pitch, sustained nystagmus was observed when the gravitational vector was approximately coplanar, but not when it was normal, to the canals responding to the angular stimuli. In all three orthogonal axes, post-rotational responses were found to depend on the position, or change in orientation of the subject, with respect to the gravitational vertical.

These findings cannot be explained in terms of the conventional division of labyrinthine function. It has also become clear that the "classical" concept of vestibular behaviour will only provide an adequate explanation of responses to angular motion in the limited circumstances where this is not accompanied by changes either in magnitude or direction of the concomitant linear acceleration. Various mechanisms to

account for the experimental observations have been critically evaluated, and the conclusion reached that it is unlikely that the canals are influenced directly by linear (gravity) accelerations. More probably the experimental observations, both per and post rotation, can best be explained by central interaction processes, mediated principally through the otolith organs, in which gravireceptor afferents modify inappropriate signals from the semicircular canals. Irrespective of the precise nature of these mechanisms, the experimental findings have relevance to problems in aerospace medicine, as well as practical implications, which are briefly considered.

In aviation combinations of angular and linear accelerations frequently occur, particularly in small high performance aircraft, and in these circumstances erroneous information generated by inappropriate signals from the vestibular receptors (especially illusory sensations of turning) are a frequent cause of spatial disorientation in flight. In this condition, the illusory vestibular sensations conflict with other sensory information, and may cause uncertainty about position or altitude, or in extreme situations even dictate the pilot's control of his aircraft, leading to serious and sometimes fatal consequences. A correct appreciation of vestibular behaviour in such circumstances, and particularly of potential modification of inappropriate canal responses by linear

acceleration, may therefore be of value in understanding and predicting the time course and magnitude of misleading sensations both during and following angular motion in flight. The picture is complicated, however, not only by the interaction between linear and angular accelerations, but also by the fact that the threshold for perception of these sensations is not stable, but alters considerably according to the pattern of stimulation of vestibular and other somaesthetic receptors.

The situation is quite different in space flight, where gravitational acceleration is effectively absent under weightless or "zero-g" conditions. Extrapolation of laboratory observations made in the presence of a gravitational field, to the weightless state, is not without considerable limitations. However, if linear (gravitational) acceleration is important in determining the pattern of vestibular responses, although there is no evidence from manned space flights which have been carried out to date, that weightlessness per se affects the behaviour of the semicircular canals (Bodin 1966), the results of the present study imply that in a "zero-g" environment responses to angular motion will differ from those observed on the earth. It may also be inferred from the experimental findings that, since gravireceptor input will be greatly reduced in the weightless state, there would be less inhibition of inappropriate vestibular signals, and in

consequence if the space vehicle were subjected to any form of rotation (inadvertent or planned) spatial disorientation might develop more rapidly. This has particular relevance to the manned orbital laboratories which NASA and USAF propose to launch in the near future, for it is intended that these 'long stay' vehicles will systematically rotate to produce artificial gravity (Billingham 1966 - personal communication).

However, the present study does not justify more than tentative speculation as to possible implications of the experimental findings to practical problems of aerospace medicine. A fuller understanding must await more detailed elucidation of the complex inter-relationship between the action of linear and angular accelerations on vestibular receptors. In this respect, the value of further human experiments may be limited, and animal investigations in which unitary activity of ampullary and macular receptors can be recorded discretely more valuable, for where reflex eye movements or sensory phenomena are used as indicants of vestibular behaviour incontrovertible evidence of the relative contribution of canal and otolith mechanisms will be difficult to obtain. However, more detailed investigation of vestibular responses to rotational stimulation under weightless conditions than have already been made (Jackson and Sears, 1965), both in animals and man, would also be of value and considerable practical importance.

In spite of numerous observations and the ingenious experimental studies of vestibular function undertaken by many workers, our present state of knowledge is still limited and indefinite; the trend however is towards increasing evidence with a uniformity of interpretation which gives grounds for optimism. On the vexed question of canal via otolith mechanisms it may be noted that experiments which suggest a canal hypothesis are invariably open to other possible interpretations; many of those which favour the otoliths, in contrast, are less open to explanation in other ways.

Much still remains to be done, and further work will require the co-operation of physiologists, otologists, physicists, neurologists and histologists if we are to continue to advance from the present state. The unique advantages offered by the environment of space flight must not be neglected, and it is to be hoped that NASA will pursue their present vestibular research programme (Billingham 1968 - personal communication) to the full.

APPENDICES

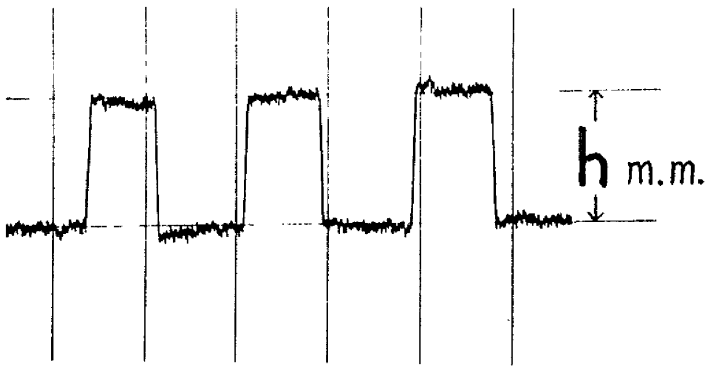


Figure A.1

EOG record showing typical calibration 'notches', obtained by the subject performing alternate eye-movements in the plane of rotation (vertical displacement of trace on the record) every sec, between two lights approximately 10^{o} apart. Several 'notches' were routinely recorded, and their average height (h mm.) determined.

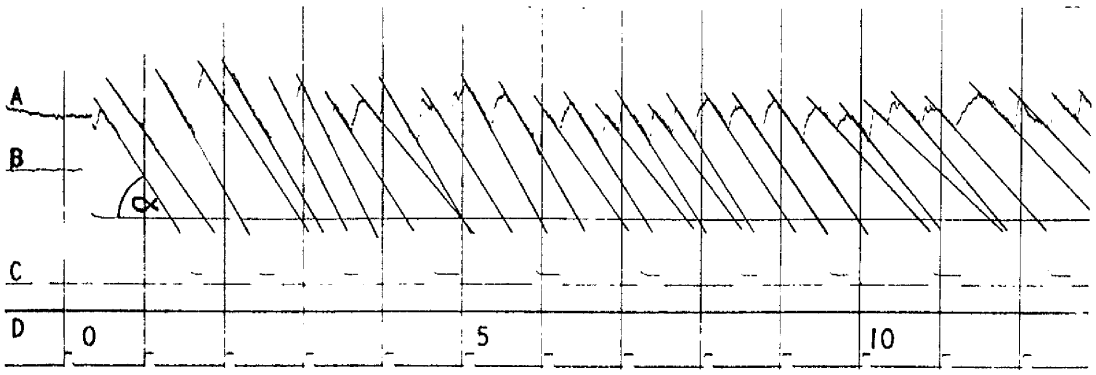


Figure A.2

Record of post-rotational nystagmus (A), with lines ruled through the slow phase component of each beat to enable their inclination (α) to the x axis (tachogenerator trace (B) on this record) to be measured. (Other traces: C subject responses; D not in use; time markers at 1 sec intervals.)

APPENDIX 1

ANALYSIS OF EYE-MOVEMENT (ELECTROCULOGRAM) RECORDS

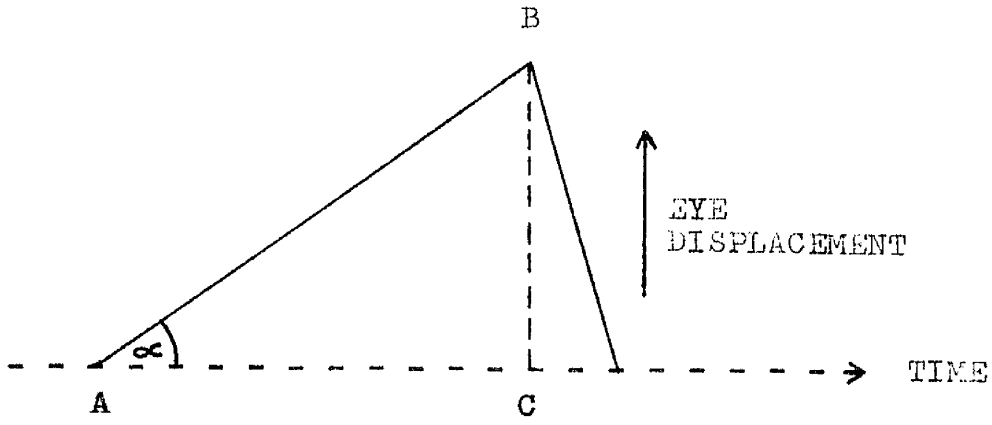
A. Procedure for Calculating the Velocity of Slow Phase Components of Nystagmus

Before and after each experimental run, subjects performed calibration eye-movements by fixating alternately (about once a second) on each of a pair of small lights, which subtended a known angle θ (approximately 10°) in the plane of rotation. These eye-movements were recorded as a series of rectangular 'notches' on the EOG film (Fig A.1). The average height (h mm.) of the calibration 'notches' for each nystagmus record, corresponding to the known angular eye-displacement (θ°), was measured with a ruler. Each mm. of vertical displacement on the record was thus equivalent to an eye-movement of $(\theta/h)^{\circ}$.

Typical recordings of post-rotational nystagmus are shown in the main results sections, e.g. Figs 5.2, 5.13, 5.14. These records were analysed in the following manner. A line was drawn through the slow phase component of each identifiable nystagmic beat, and the inclination (α) of each line to the x axis (tachogenerator trace, time marker or edge of film) measured with a protractor, as shown in Fig A.2. The speed of the film through the recorder (assumed constant) was also

determined, by measuring the average interval between 1 sec time markers (t mm.). Each mm. along the record was thus equivalent to 1/t sec.

Consider now a typical nystagmic beat, with slow phase component AB inclined α° to the horizontal:



In the time interval AC (= AC.1/t sec), the trace moved upwards on the record through a distance CB mm., representing a slow phase eye-displacement of $(CB.\Theta/h)^{\circ}$. Hence the eye-velocity during this movement, $\omega^{\circ}/sec = \left(\frac{Distance}{Time}\right)$, was:

$$\omega = \frac{(CB.\Theta/h)^{\circ}}{(AC.1/t)sec} = \frac{CB}{AC} \cdot \frac{\Theta t}{h} \ ^{\circ}/sec$$

$$As \ \frac{CB}{AC} = \tan \alpha$$

$$Then \ \omega = \frac{\Theta t}{h} \cdot \tan \alpha^{\circ}/sec.$$

$(\Theta t/h)$ is conveniently regarded as a calibration factor (F), since it need only be determined once for each post-rotational nystagmus record. The velocity of slow phase

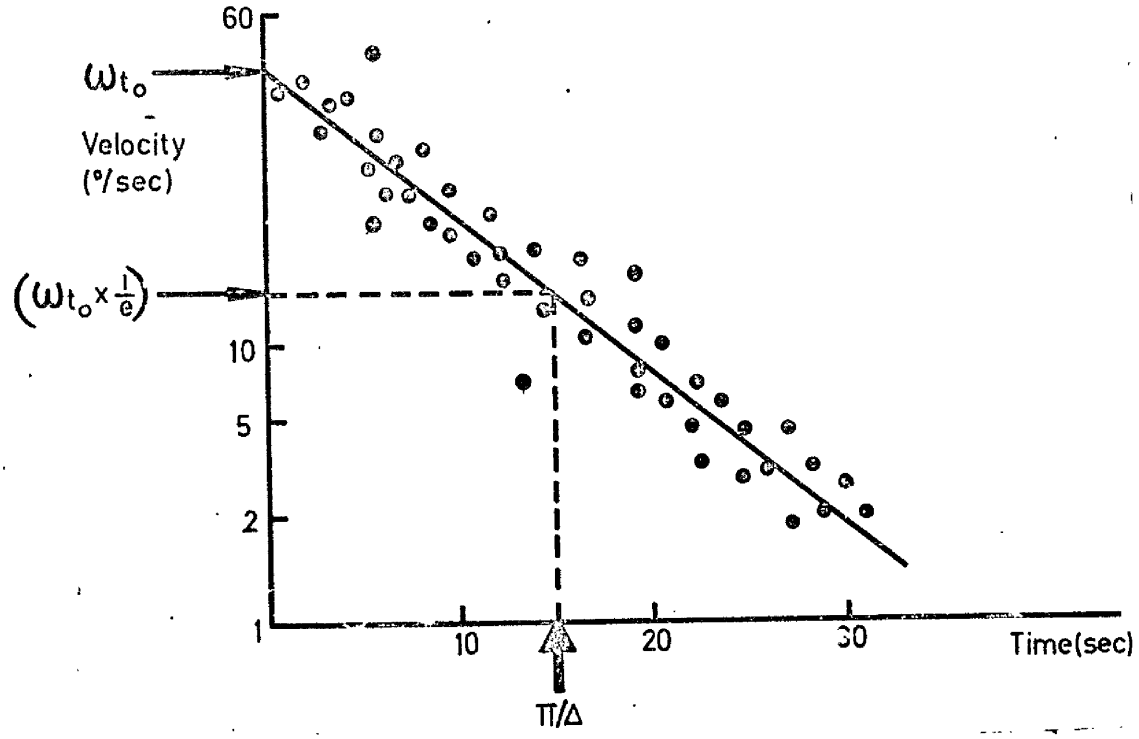


Figure B.1

Log-linear plot of slow phase velocity of post-rotational nystagmus against time after stopping. The 'best fit' straight line has been drawn in and extrapolated to meet the ordinate axis at ωt_o. The method of obtaining a numerical value for the Time Constant of Decay (π/Δ sec) is clearly illustrated.

nystagmus was then computed, after measuring the slope of each slow component (α), from the formula

$$\omega = F. \tan \alpha^{o}/sec$$

B. Analysis of the Pattern of Decay of Nystagmus: Calculation of Time Constant of Decay (τ/A) and Initial Slow Phase Nystagmus Velocity (ωt_o)

The decay of nystagmus is exponential. Slow phase velocity is therefore plotted on a logarithmic ordinate scale against time after stopping (Fig B.1). The time of occurence of each beat is taken as that of the mid-point of the slow phase component (Fig A.2).

An advantage of this form of analysis is that it is not necessary to measure every nystagmus beat. Provided a sufficient number are taken, reasonably uniformly dispersed in time (e.g. alternate or one in three beats may be adequate) the resulting plot, though showing some scatter, will be essentially linear, and it is not difficult to draw, by eye, a good 'best fit' straight line. This is extrapolated to intersect the ordinate axis at a point which corresponds to the peak initial slow phase velocity (ωt_o). Very occasionally a record contains only a few scattered nystagmus beats, and in these situations the 'best fit' straight line should be obtained by calculating the regression equation. It is most unusual to have to do this.

The time constant of decay is simply a particular measure of the 'slope' of the log-linear nystagmus velocity plot: by definition the abscissa value corresponding to the point on the ordinate scale at which the initial slow phase velocity

has fallen to 1/e of its original value, i.e. a velocity of ωt_o x 1/e (ωt_o x 0.368). This is shown clearly in Fig B.1.

The effect of different magnitude stopping stimuli on initial peak velocity and 'slope' value has already been discussed (Part 3, section 5(e), Fig 3.5).

It may be noted also, and will be apparent from Fig B.1, that the more rapid the decay of nystagmus, the steeper the 'curve' and the smaller the 'slope' value.

APPENDIX 2

Preparation, Care and Application of Electrodes in Nystagmography

The technique of electronystagmography is described in Part 3, section 3. E.M.I. rubber suction cup electrodes (Shackel, 1957) were employed. These have the appearance of a soft rubber 'bell', with the actual electrode a short blunt (silver) pole in the centre. When properly applied, the suction of the rubber casing grips the skin securely, and also pinches it up centrally to press firmly on the tip of the metal pin. Meticulous preparation is important for maximum accuracy. The procedure for preparation and application of the electrodes was as follows:

1. Rinse electrodes in distilled water.

2. Soak for 15 - 30 mins. in 1% sodium chloride solution, with leads shorted together, taking care that no air bubbles are trapped within the rubber cups.

3. Chloride the electrodes for about 10 - 15 sec., by passing a current not exceeding $\frac{1}{2}$ m.a. through them. This deposits a thin coat of silver chloride on the silver pole of the electrode, thus providing a uniform surface coating on the 'active' tip of each, which helps to reduce to minimum any possible standing potential between the electrodes when applied to the subject. Currents greater than $\frac{1}{2}$ m.a. should

not be used, as this may impair the quality and crystalline structure of the deposited silver chloride coating.

4. Immediately before applying electrodes, remove from soaking and shake off surplus drops of saline solution.

5. Clean the appropriate areas of subjects skin, first by simple abrasion, then with alcohol, and allow to dry.

6. Half fill each electrode cup with 1% sodium chloride electrode jelly.

7. Squeeze the cup until jelly protrudes, press firmly to skin and gently release. The electrodes should then adhere securely by suction. The area of skin chosen for application must be flat; e.g. if at the outer canthi it should be sufficiently far back to be free of skin creases.

8. After use, squirt with distilled water to remove saline jelly, allow to dry and store in a clean container placed in a cool place.

9. The electrodes must always be handled with clean non-greasy fingers and the silver/silver chloride pole should never be touched. If they become dirty, clean and degrease with carbontetrachloride.

Drift. With the above preparation, which is essential for accurate DC recording, zero drift did not exceed 30 microvolts in one minute, and was usually less than 10 microvolts in one minute.

Very occasionally, with some subjects or in certain experimental situations, drift or changes from the isoelectric line occured in considerable excess of these values. A manual 'back-off' circuit was provided on the preamplifier to cope with such contingences.

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It is regretted that owing to unavoidable circumstances a very small number of references have inadvertently been omitted, and a few slightly abbreviated.